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STUDIES ON THE MAMMALIAN KIDNEY

BY

IVAR SPERBER

UPPSALA 1944
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STUDIES ON THE MAMMALIAN KIDNEY

INAUGURAL DISSERTATION

BY

IVAR SPERBER

FIL. LIC. G.-H.

BY DUE PERMISSION OF THE PHILOSOPHICAL FACULTY OF THE UNIVERSITY OF UPPSALA TO BE PUBLICLY DISCUSSED IN THE ZOOLOGICAL INSTITUTE, ON APRIL 21, 1944, AT 10 O'CLOCK A. M., FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

UPPSALA 1944

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Studies on the Mammalian Kidney.

By

IVAR SPERBER
(Uppsala).

With 3 plates and 29 figures in the text.

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Preface.

In publishing this investigation it is my pleasant duty sincerely to thank my teacher, the Rector of the University, Professor Nils von Hofsten for the interest and helpfulness he has shown in every respect.

My thanks are also due to my teacher Professor Sven Ekman, and to the Director of the Zoological Institute, Professor Sven Hörstadius.

Most of the preserved kidneys examined belong to the collections of the Zoological Institute, Uppsala. For the opportunity of examining some material in the collections of the Museum of Natural History in Stockholm I am obliged to the Director of the Vertebrate Department of this museum, Professor Hialmar Rendahl.

On some points concerning the statistical methods I have had the opportunity of consulting Professor Gunnar Dahlberg, for which I tender my thanks.

To Miss Amy Wästfelt, who has drawn the figures in Indian ink, and to Mrs. Carolyn King, who has revised my style, I also wish to express my gratitude.

Uppsala, March 1944.

Ivar Sperber.

I. Introduction.

General account of the form of the kidney and the nephrons.

In this paper descriptions are given of the macroscopical and microscopical anatomy of the kidneys of a number of mammals, and some pertaining problems are discussed. To make clear the terms used a general account of the structure of the mammalian kidney is given below as regards the features investigated.

The form of the kidney. The mammalian kidney consists of cortex and medulla. This division refers mainly to differences visible to the naked eye. The medullary rays are as usual included in the cortex, though their structure agrees in essentials with that of the medulla. The medulla usually consists of two layers, the inner zone and the outer zone (fig. 1 *A*). The outer zone may be subdivided into two parts, the inner stripe and the outer stripe (Peter 1909). (Heidenhain 1937 includes the outer stripe in the cortex. He also creates an entirely new terminology for the other layers. This does not seem appropriate, as the inner boundary of the cortex in this case would be mainly indistinguishable macroscopically. As Peter's terminology has already been used by several writers and is suited to both macrosopic and microscopic investigations, alterations seem unnecessary.)

There is considerable variation in the shape and structure of the mammalian kidney. To facilitate the description of the forms, these may be divided into some types, descriptions of which are given below. These types mainly agree with those of previous authors, especially Gerhardt (1911, 1914).

1. The kidney surface is even, or has slight grooves. There is a medial concavity, the hilus, where the ureter and the blood-vessels enter the kidney. The hilus leads into a space, the sinus renis, which contains the renal pelvis (fig. 1 *A*, *pv*). The medulla is undivided and forms a papilla. The collecting ducts of the kidney open on the apex of the papilla, forming the area cribrosa (fig. 1 *A*, *a.c*). The papilla projects into the pelvis, which often has processes projecting into the medulla. Alternating with the processes there are elevations, somewhat like buttresses, at the basis of the papilla. These are often called pyramids, but to

avoid confusion, they are properly named secondary pyramids. (Other names are: Anbaue, Seitenwülste (Gerhardt), Nebenwülste (Müller 1883), Nebenwarzen (Hyrtl), Pseudopapillen (Brasch 1909).) It may be mentioned that Gerhardt calls a pelvis with processes 'branched'; this can cause confusion.

2. Closely allied to the kidney with a papilla is a type where the

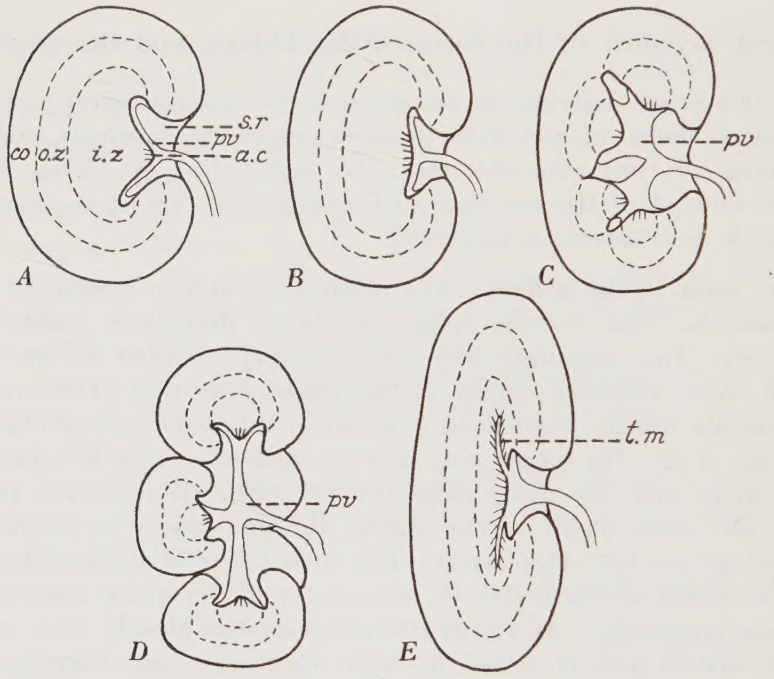


Fig. 1. The mammalian kidney types. *A* Simple kidney with a papilla. *B* Crest kidney. *C* Kidney with several papillae. *D* Renculi kidney. *E* Kidney with tubi maximi. *a.c* area cribrosa, *co* cortex, *i.z* inner zone, *o.z* outer zone, *pv* pelvis, *s.r* sinus renis, *t.m* tubus maximus.

papilla is replaced by a crest (fig. 1 *B*). The crest, too, may be absent, and then the area cribrosa lies on an even or concave surface, constituting the lateral limit of the pelvis. The area cribrosa is not round as in the preceding type, but oval.

3. The medulla is divided into two or more (primary) pyramids (fig. 1 *C*). Each pyramid forms a separate papilla or crest. The cortex, however, is undivided as in the preceding types.

4. Structurally, the kidney of this type consists of several parts, renculi, which are organized entirely as small kidneys (fig. 1 *D*). The pelvis is branched, as is often the case in the type with several papillae also. Externally, kidneys of this type are often lobated.

5. The kidney of this type is usually a simple kidney with even surface and undivided medulla. Part, at any rate, of the collecting ducts join large ducts, tubi maximi, mostly two, which open into the pelvis, in most cases at the extreme ends of the area cribrosa (fig. 1 *E*).

The tubules. The shape and course of the renal tubules have been investigated repeatedly in the nineteenth century. Later, especially Peter (1907, 1909, 1927) and Huber (1911, 1917, 1928, 1935) have investigated this subject. Peter (1909) gives a full account of the earlier papers.

Below I shall give a general account of the tubules, mainly following Peter and Huber. The terminology is somewhat altered, chiefly in agreement with Grafflin (1937).

Policard (1912) is of the opinion that the subdivision of the nephrous made by Peter overreaches the observable facts. In the discussion on this matter I agree entirely with Peter. The differences between the segments which appear in maceration preparations cannot be explained as artefacts. They are far too regular. There is little difficulty in finding the distinct segments in sections, too (cf. also Okkels 1929).

v. Möllendorff (1930) adopts Policard's division and states that this is better suited as a basis for comparative studies. This is possible but Peter's scheme comprises all different segments that are discernible, which is not the case with that of Policard. Thus Peter's system seems best suited to investigations within the *Mammalia*.

The tubules may be divided into the nephrons and the collecting tubules.

A nephron begins with Bowman's capsule, which surrounds the glomerulus. The form of the capsule is variable. If, as seen under the microscope, the diameter passing through the beginning of the proximal tubule is the longest diameter, the capsule is said to be oval. If this diameter is the shortest one the capsule is termed transversely oval, and the capsule is called round when the contour is more circular. The capsule may, of course, also be flattened, but as this is difficult to see, it is mentioned only when this circumstance is marked. The epithelium of the capsule is low and transparent.

The next part of the nephron is the proximal tubule (fig. 2 *A*). At the beginning of the proximal tubule there is sometimes a short constriction, the neck. The cells of the proximal tubule contain rod-like mitochondria, and possess a brush border. In maceration preparations this segment is distinguished by its high, relatively opaque epithelium. The first part of the proximal tubule mostly consists of some loops near the capsule, and is termed pars convoluta. The rest of the proximal tubule, the pars recta, descends in a more or less straight path towards the medulla.

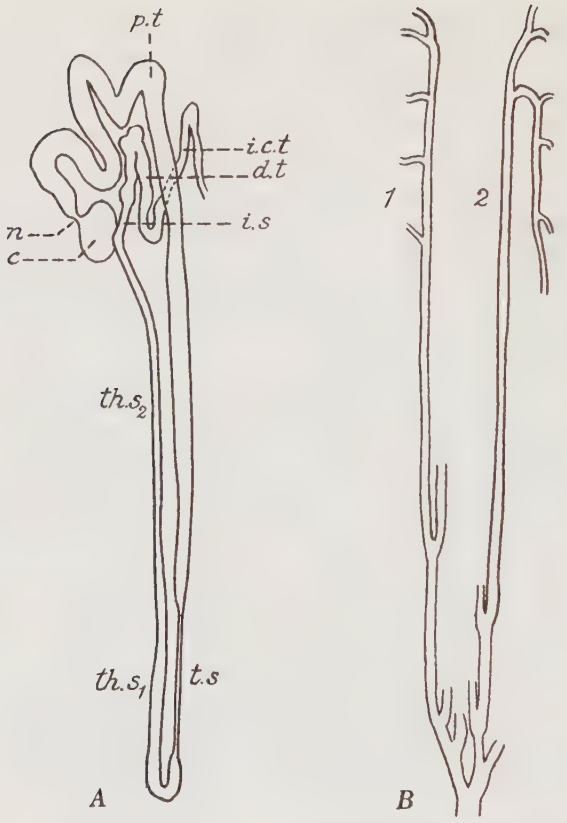


Fig. 2. Scheme of *A* nephron, *B* collecting tubules. *c* capsule of Bowman, *d.t* distal tubule, *i.c.t* initial collecting tubule, *i.s* intercalated segment, *n* neck, *p.t* proximal tubule, $th.s_1$ thicker part, $th.s_2$ thinner part of thick segment, *t.s* thin segment. *1* collecting tubule with direct junctions, *2* d:o with arcade.

The transition into the next segment of the tubule, the thin segment, normally occurs at the boundary between the outer and the inner stripe. The thin segment has a small diameter, and is very transparent, as its epithelium is very low and the granules are few.

The next part, the thick segment, again, presents a high epithelium, containing rod-shaped mitochondria, but without a brush border. This segment is often differentiated into a thicker proximal part and a thinner, more transparent, distal part. The thicker part is mostly situated in the outer zone, and the thinner part in the cortex. The transition is gradual.

Together with the pars recta of the proximal tubule the thin segment and the thick segment form the loop of Henle. The loops are said to be long when they turn in the inner zone of the medulla. Those loops which turn in the outer zone are called short, and if there are nephrons whose loops turn in the cortex, they are called cortical nephrons. In

the latter the thin segment may be absent. The long loops always turn within the thin segment, and the short loops mostly turn in the thick segment.

The thick segment returns to the capsule, and touching the capsule it passes into the distal tubule. This segment is tortuous and usually thicker and less transparent than the thick segment, but otherwise of about the same structure. The first part of the distal tubule, however, may show about the same appearance as the thinner part of the thick segment, and is then called the intercalated segment.

The transition into the next segment, the initial collecting tubule, is gradual and often indistinguishable. The epithelium of this segment is relatively low and transparent.

The initial collecting tubules join to form the collecting tubules, the epithelium of which, in the cortex, is quite like that of the initial collecting tubules. In the medulla it becomes higher and often somewhat opaque. In the inner zone the collecting tubules join repeatedly, mostly in pairs (fig. 2 *B*). The ducts thus formed open on the area cribrosa. The junctions between the initial collecting tubules and the collecting tubules are called peripheral junctions and occur in the cortex. In the medulla only collecting tubules join, and these junctions are termed central junctions. The peripheral junctions show two distinct forms. They may be direct, in which case the collecting tubule begins in the outer part of the cortex and descends to the area cribrosa, nephrons joining it in the cortex (fig. 2 *B*, *1*). In other cases the collecting tubule forms an arcade, that is, it starts in the lower parts of the cortex, ascends through the cortex, where some nephrons join it, and turns in the higher parts of the cortex to descend to the area cribrosa (fig. 2 *B*, *2*).

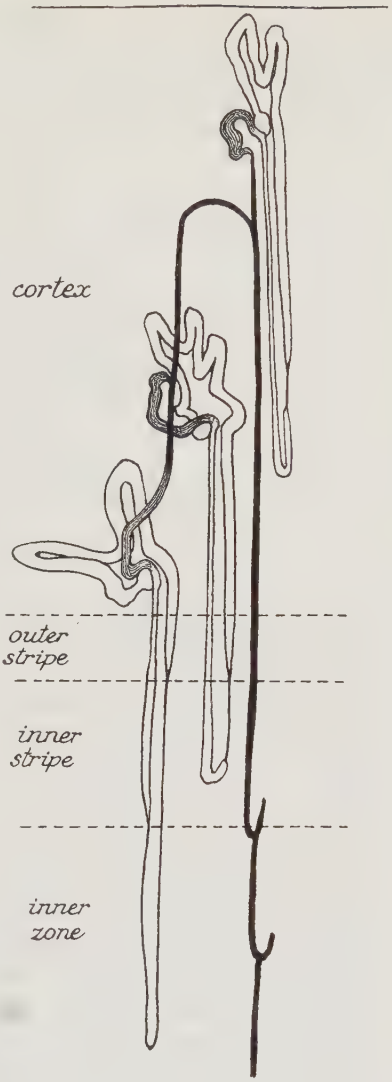


Fig. 3. Scheme of the situation of the nephrons. Collecting tubules black, distal tubules grey.

The position of the nephron segments in the kidney. The capsule, the main part of the proximal tubule, the thin part of the thick segment, the distal tubule and the initial collecting tubule are always situated in the cortex (fig. 3). In the outer zone are found the most central parts of the proximal tubules, thin segments and the thicker parts of the thick segments. Apart from collecting tubules, which are found in all layers, the inner zone contains only thin segments.

Normally, most proximal tubules end at the same level — the boundary between the outer and the inner stripe. Thus, the latter never contains any part of the proximal tubules. The zone boundary is the level at which the most centrally-reaching thick segments pass into thin segments.

As a rule the loop of a high (peripheral) nephron turns at a higher level than the loop of a deeper (more central) nephron. Small deviations from this rule are not unusual. The loops of the deepest nephrons get nearly as far as the area cribrosa.

Technique and methods.

The shape and size of the kidneys has been ascertained from fresh kidneys, when possible. In most cases only preserved material could be obtained, and then both shape and size may be altered to a certain extent. Deformation is often evident as a result of the pressure from other organs during hardening. This affects the relations between the dimensions as well as the shape itself. The measurements may be altered by swelling or, mostly, by shrinkage. These changes, however, seem seldom to be so great that a good idea of the shape and size cannot be obtained.

The thickness of the layers and the form of the papilla has been assessed from a medial section, parallel to the flattened surfaces of the kidney. Such a section is in normal circumstances easily obtained by cutting through the cortex along the largest circumference of the kidney through the hilus, and tearing the halves of the kidney apart. Such a section then generally passes through the area cribrosa. The measurements of the medulla are made from the area cribrosa, transverse to the longest axis of the kidney. Such sections of a number of kidneys have been drawn as accurately as possible and are reproduced in the special section. Of course they are not always exactly median, as the kidneys are often somewhat irregular in shape. The boundaries between the cortex and the medulla and between the zones of the medulla have also been drawn in these figures, but sometimes these boundaries are slightly generalised as it is not always possible to trace them all over the section. In cases when it has not been possible to ascertain their essential features they have, of course, not been drawn. The shape of the pelvis has most often been examined by dissection.

To investigate the tubules, pieces of kidneys have been macerated with hydrochloric acid. This technique has been employed on both fresh and preserved material. Pieces of the kidney are placed in the concentrated acid (sp. gr. 1.19) and remain there for some hours, in the case of fresh material. The pieces are then transferred to a Petri dish, with water. After some time they are ready for teasing. The tubules are now normally fairly soft. If the acid is less concentrated the pieces must remain in it longer and the tubules become more brittle. It is usually advantageous to employ concentrated and slightly diluted acid on different pieces. Sometimes still better results may be obtained by injection of the acid through the renal artery (according to Huber 1911). This often gives a very even and good result. The capsules, however, easily become detached later during dissection.

The acidity of the water in which the teasing is carried out is of some importance. If there is too much acid the tubules become brittle, and if there is too little the same result may ensue. It is, however, not possible to define the suitable acidity, as it is influenced by several factors, as age of the animal and the maceration technique.

Sometimes the preparation is more suited for teasing some days later, and often the condition of the tubules may be improved by adding a few drops of glycerine to the water, especially when the tubules are brittle. Preserved kidneys sometimes give very good macerations, but mostly the results are inferior to those obtained from fresh material. This seems especially to be the case when the kidneys have been exposed to light for considerable periods.

The tubules are dissected with glass needles. If the shape only is to be examined, it is preferable to macerate with slightly diluted acid. Material macerated with concentrated acid lends itself better to measurements, however. Long segments are then easily dissected, and often it is possible to isolate complete nephrons. The coils and loops of the tubules are also more easily stretched out, which is necessary for tolerably exact measurements.

The first measurements are made already during the dissection (under a dissecting microscope). As soon as the thin segment of the nephron under dissection is clearly recognised, it is measured with an eyepiece micrometer. When the nephron or segment is isolated it is transferred to a slide with the aid of a wide pipette. The diameters of the capsule are measured with the nephron still floating in water on the slide. Then most of the water is removed so as to stretch the tubule out on the slide. The lengths of the segments of the nephrons are now measured with the eyepiece micrometer at a magnification of about 200 ×. The thickness of a segment is obtained as the mean of several measure-

ments at separate points, at a magnification of about 350 ×. Sometimes the nephron or the segment has been drawn at a known magnification, and the measurements have been made from the drawing.

The following sources of error seem to be most important:

1. The tubules shrink or swell during maceration or later. This is almost always the case. After maceration with weak acid there is generally some shrinkage, and it may be great in some cases. Swelling most often occurs after maceration with strong acid. The acidity of the water in which the dissection takes place has, however, the most striking effect. A segment may exhibit variations to an extent of 50 per cent due to this factor. The extreme deviations are of no importance as a source of error, however, since in these cases the material is not fit for dissection.

To eliminate this source of error as far as possible the following procedure has been used: On the piece that is to be macerated the thicknesses of the cortex and medulla are measured, or their sum. Immediately before teasing the same measurements are made. Thus, gross variations in the thickness of the layers are discovered and measured. These measurements are, however, not very exact, and there is probably not a strict relation between the changes of the different segments as their structure is different. Considering this, deviations less than ten per cent of the initial value have been disregarded. Greater changes are mentioned in the description of the tubules in the special section, and in calculations of absolute values a correction has been applied.

Earlier investigators have not tried to estimate this source of error. Peter and his co-workers (1909, 1927) and Huber (1911, 1917) seem to have believed the dimensions of the tubules to be the same after maceration as before. Foote and Grafflin (1938), on the other hand, are aware of the probability of changes, but make no attempt to obtain the true values.

Swelling and shrinkage may, of course, occur after dissection also. Especially during drawing, and if the tubules are subjected to long series of preparations, relatively large variations may occur which are not possible to assess. This is probably the case when the measuring is preceded by mounting in glycerine-jelly (Steinbach 1926, Peters 1928). These errors are probably best avoided by measuring the tubules lying in water on the slide direct with an eyepiece micrometer. It seems to me that this should more than compensate the somewhat lower degree of exactness in measuring of this method as compared with the measuring from drawings.

2. The length and thickness of the tubules may be altered by the teasing. The tubules, however, are normally so elastic that they resume

their earlier shape even after severe distortion. The thin segment seems to be most liable to permanent lengthening, and to control this, this segment is measured as soon as possible (cf. p. 259). When the connective tissue is tough and the tubules are very soft after maceration the other parts of the nephrons may also be influenced by this factor, and such material has been avoided, if possible.

The capsules are very easily flattened through any pressure. This I have tried to avoid by measuring the capsules floating in the water, but it is possible that the largest capsules have been somewhat flattened all the same. The latter also have a tendency to present their largest surface to the observer when they lie on a slide, which also tends to raise the values of their dimensions as compared with the true values.

3. The length of the loops is underestimated, as they do not all lie in the same plane. This applies mainly to the proximal and the distal tubule. This source of error is diminished by the use of relatively soft material. (The error due to foreshortening must have been considerable in the measurements of Peter, as he realises, and is probably considerable also in the data given by Pai 1935.)

4. The deficiency of exactness in the measuring. This factor is important, but duplicate measurements normally agree to within 5 %. This error is diminished by measuring a greater number of tubules.

If possible entire nephrons have been isolated, as these give information not only as to the size of the segments, but also as to the proportion of them in relation to each other. It is in many cases exceedingly difficult or impossible to avoid breakage, especially in the thin segment, even when the maceration is successful. In such cases it has often been possible to see the thin segment in connection with the other segments, before the breakage. In this case the nephron has been treated as if intact. In other cases the connection between the proximal tubule and the distal parts has been considered sufficiently established if the thick segment is attached to the capsule at its transition into the distal tubule. Grafflin (1939, p. 708) discusses the justness of this procedure. In most kidneys it is easy to ascertain that the thick segment touches and is attached only to the capsule that belongs to the same nephron as the segment itself. Where the cortex is thick and the connective tissue tough it sometimes happens that the thick segment is attached to more than one capsule. Then the above-mentioned procedure cannot be adopted, and this is also impossible when the attachment is lost during maceration or dissection. This occurs especially after injection of the acid according to Huber.

The measurements have been used as the basis for several calculations. By multiplying the two measured diameters of the capsule an equivalent of the surface of the capsule has been obtained. This might seem too great an approximation, and it might also be assumed that this method is inferior to the one employed by v. Möllendorff (1922) and Peters (1928). They measured the diameter parallel to the line of vision also. It seems to me that the accuracy in the measurement of this diameter is so low that the errors introduced thereby probably more than outweigh the theoretical advantages of taking all three dimensions in the calculations. It is also evident that, when the capsules have approximately the same shape, no important error is introduced by assuming that the third diameter is proportional to the other two. If, however, systematic variations in shape occur, this error is of course important. Thus, flattened capsules cannot well be compared with spherical ones.

On analogous reasons it seems unnecessary to measure the thickness of the tubules in more than one plane. The surface equivalent has accordingly been obtained as the product of the length and the mean breadth of the segment. For each proximal tubule connected with its capsule, the ratio of the surface equivalents of the proximal tubule and the capsule has been calculated, and given in the tables under the heading "Ind."

The mean length and thickness of the segments have been obtained as the mean of the measurements. Sometimes these means have been corrected, since in some cases relatively too many long, deep nephrons have been measured. Such corrections are mentioned in the description of the species.

The mean length of the thin segment has sometimes been calculated as follows. After maceration a pyramidal piece, containing a small part of the cortex and the corresponding part of the medulla, is teased from the preparation. This piece should include the whole length of all the loops of the nephrons contained in it. The thickness of the inner zone is measured, and then the innermost part of the inner zone is removed. It is then usually possible to dissect a short segment of each of the loops cut at this level and count the loops. If the thickness of the inner stripe is a mm, and the distance from the zone boundary to the level where the counting has been made is b mm, the minimal length of the thin segments reaching below this level is $a + 2\,b$ mm. The mean length is taken as the average of the longest and the shortest loop cut. Thus the whole inner zone of the piece is gradually removed, and the mean length of the thin segments of the long loops may be calculated. The length of the thin segment of the short loops is as a rule easily measured, and if the relative abundance of short and long loops is known the mean length of the thin segment may be calculated. This method does not give very accurate figures, but its results may be used for purposes of comparison.

When means have been calculated for the proximal tubule and the thick segment their standard error has normally also been calculated. It is doubtful if this is always justifiable. The measurements are often very few, and sometimes the distributions are markedly skew. The standard error has, however, been given, as in any case it gives an idea of the significance of the means. In most cases high, middle, and deep nephrons have been selected and measured in numerical proportions approaching as closely as possible the conditions prevailing in the kidney. This procedure has been applied because the length of the nephrons and their segments is often correlated with their position in the cortex. The mean length of the segments is more exactly estimated in this manner than by the mean of random samples. The standard error of the mean is also affected by this procedure. Below is given an example of how the significance of the mean and the standard error are influenced by the procedure.

The majority of the forms examined shows relatively uniform circumstances. In one case (*Mus flavicollis*, "young male", table 22 a, p. 308) the material is large enough to permit of a statistical analysis. In this specimen small samples (about 9 nephrons) have been taken in such a manner that they have a composition (of high, middle and deep nephrons) comparable to the entire kidney. The proximal tubules in fifteen such samples have been measured. For each sample the mean and the standard error has been calculated. The mean of these means and its standard error has also been calculated, and also the mean of the whole material and its standard error and standard deviation. As is to be expected, the mean of the whole number of primary data, 3.541 ± 0.045 mm, and the mean of the group means, 3.532 ± 0.030 mm, agree well. The standard error is lower when the mean is calculated from the group means. This indicates that these group means are better estimations of the mean of the whole material than those of random samples would be. This is to be expected, as the groups are selected so as to be representative of the whole material. From the standard deviation of the data in the total material, ± 0.529 mm, the standard error of the means of random samples of nine proximal tubules has been calculated. It is ± 0.176 mm. This standard error is about the same as the average of the standard errors obtained for the selected samples, $\pm 0.169 \pm 0.010$ mm.

Thus the means of samples selected so as to be representative, are better estimates of the true mean than are the means of random samples. As their standard error is as large as that of random samples the means of selected samples are more reliable than their standard error would indicate. As this example is typical of most forms examined it seems that the standard errors calculated may be assumed to indicate the significance of the means as safely as standard errors of the means of random samples.

II. Special section.[1]

Monotremata.

Ornithorhynchus anatinus Shaw.

Material. The kidneys of two specimens in alcohol.

Form. In one of the specimens both kidneys measure about 30 × 18 × 12 mm. The pelvis consists of a small flattened cavity. The area cribrosa is oval and lies either on a small crest, that projects into the pelvis, or in the lateral wall of the pelvis (fig. 4 *A*, p. 271). The latter has no processes. The boundary between cortex and medulla is indistinct, as there are many thick medullary rays projecting into the cortex. The cortex is about 4 mm thick, and the medulla 4.5 mm. There is no visible inner zone. After maceration the outer stripe becomes distinct. It is about 1.5—2 mm thick.

The tubules. After maceration the material is very brittle, especially the outer parts of the cortex and the distal tubules. It has, however, been possible to note the following facts. There are a great many cortical nephrons, but no or at any rate very few nephrons with long loops. The capsule and the proximal tubule are of the usual shape. The pars recta is always well developed, even in the deepest nephrons, and it often constitutes as much as half the proximal tubule. The transition into the thin segment occurs at very varying levels. Very few proximal tubules reach the stripe boundary; thus the latter is relatively indistinct even after maceration. There are thin segments in most nephrons, and only in the highest cortical nephrons is it absent, but it is mostly very short. I cannot definitely say if there are loops which turn in the thin segment, as the innermost part of the medulla consists mainly of very tough connective tissue. However, the loops that reach this zone are very few. The thick segment is very markedly differentiated into a thicker and a thinner part, except in the highest nephrons. The distal tubules are relatively thin and without projections. If there are initial collecting tubules, they are very indistinct. The collecting tubules are thin (about 0.020 mm in the cortex and the outer parts of the medulla, less than 0.050 mm in the inner parts of the medulla). As the central

[1] The nomenclature and system of WEBER (1928) have been used when possible.

junctions occur even in the middle and lower parts of the cortex, there is no marked difference between central and peripheral junctions. It is very difficult to examine the peripheral junctions as these are situated in the outer parts of the cortex. It is certain, however, that there are no typical arcades.

Monotremata, survey of the form of the kidney.

The statements on the kidney of *Ornithorhynchus* are rather inconsistent, as are also those on the kidney of *Echidna*. The latter has been thoroughly investigated by Zarnik (1910). According to Zarnik there is a distinct pelvis, and also a very low papilla with a shallow concavity, where the area cribrosa is situated. Hyrtl (1872), who has investigated the shape of the pelvis, seems to agree with Zarnik. Both Hyrtl and Zarnik give figures of their findings, and the latter had two fresh kidneys at his disposal; thus his statements have great weight. Accordant statements are given by Gerhardt (1911, 1914) and Owen (1847 b), too. Cuvier (1840), however, states that there are four papillae, but this seems highly improbable, though it is difficult to imagine how he may have reached such an opinion. The value of his statement is, however, diminished by his obviously erroneous statement that the hedgehog kidney has five papillae. What he meant by papilla is somewhat obscure.

Gegenbaur (1901) states that there is no papilla, the ureter branching directly without forming a pelvis. As this description is contrary to all other statements and as there are no details given and no drawing, it does not seem to me that it deserves any consideration.

Hyrtl (1872) has investigated the form of the pelvis in *Ornithorhynchus*, and his description and figure are in accordance with my findings. The statements of Gegenbaur (1901) are very divergent in this species also. He is of opinion that the collecting ducts open into the pelvis everywhere, but in addition to this he says there are some larger ducts. He gives a drawing of this species. Gerhardt (1911) is of the same opinion, and in support of it he cites, besides Gegenbaur, Home (1801 a and b) and Meckel (1826). The one paper by Home "Description of the anatomy of *Ornithorhynchus hystrix*" handles *Echidna*; the other, though it refers to *Ornithorhynchus*, contains nothing about the interior structure of the kidneys. I have not had the opportunity of studying the paper by Meckel, but Owen (1847 b) reproduces a drawing of the uro-genital organs of *Ornithorhynchus* according to Meckel. From this it is evident that Meckel's findings are quite in agreement with those of Hyrtl and myself. Owen too (op. cit.) describes the kidneys in

accordance with this view, but it is not clear if, in this respect, he only relies on MECKEL, or if — as seems more probable — he has made personal investigations.

In 1914 GERHARDT gave a figure of a section through an *Ornithorhynchus* kidney, but from this it is only clear that the kidney was not well preserved, as he himself mentions. He is aware that it is extremely difficult to form a well-founded opinion on such material, which fact I wish to emphasize.

From the above it seems clear that both the existing forms of *Monotremata* possess simple kidneys, whose pelvis is simple. In *Echidna* there is a low papilla, in *Ornithorhynchus* there is a crest. Both of them have cortical nephrons, and the inner zone of the medulla is but poorly developed. In connection with this the thin segment is short.

Marsupialia.

Sminthopsis murina (Waterh.).

Material. One pair of kidneys in alcohol.

Form. Size: $9 \times 5 \times 4.5$ mm. The papilla is pointed but not very long (fig. 4 *B*, p. 271). After maceration the cortex measures 1.0 mm, the outer zone 1.4 mm and the inner zone 2.4 mm. There is no swelling as compared with alcohol material.

The tubules. BOWMAN's capsule has a very thin, transparent epithelium, but where the proximal tubule begins it is considerably thicker and less transparent (Pl. 1, fig. *2*, *3*). The capsule is most often oval. The proximal tubule begins without any indication of a neck. It is fairly evenly coiled and its surface is relatively smooth. The most proximal part is frequently somewhat thicker, and the most distal part somewhat slenderer, than the rest of the proximal tubule. The pars recta of the high nephrons is long, and the convolutions of the pars convoluta rather irregular. (Pl. 1, fig. *1*.) The pars recta of the deepest nephrons, which are much longer than the others, is short, and the pars convoluta consists of almost straight segments parallel to the cortico-medullary boundary (Pl. 1, fig. *2*). The transition into the thin segment is usually rather sudden, exteriorly also. This transition occurs at slightly different levels, higher in the highest nephrons. The thin segment has a very low, transparent epithelium which is, however, often somewhat higher at the transition to the preceding and the following segment. The thick segment is distinctly differentiated into a thicker part, chiefly restricted to the outer zone, and a thinner and more transparent part in the cortex. The short loops turn in the inner half of the outer zone, normally in the thick

segment (Pl. 1, fig. *1*.) The distal tubule, which begins where the thick segment touches the capsule, is thicker than the distal part of the thick segment. The transition is usually distinct and marked. The contour of the distal tubule is rather even, and the transition to the initial collecting tubule is gradual. The proximal part of the collecting tubules is slightly thicker than the following cortical part, which is usually 15—20 μ thick and fairly transparent. The peripheral junctions are never typical arcades, but occasionally a high nephron may join the collecting tubule below a deep one, so as to reverse the normal order. The central junctions lie in the inner zone, the peripheral ones only in the outer half of the cortex. Three to five nephrons join to form one collecting tubule.

Table 1.[1] *Sminthopsis murina, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	75×60	1100×30	620× 9	1300	850×25	30	17	35	18	7.3
h	68×60	1300×30	400× 8	1150×27	600×28	38	12	33	17	9.6
h	75×69	1350×35	800	1650×30	750×30	30	18	36	16	9.1
m	68×55	1400×34	800	1650×24	550×26	32	18	37	13	12.7
h	83×75	1400	600	1500	680	33	14	36	16	
h	75×56	1430×30								10.2
m	90×65	1450×35	600× 8	1450×26	700×29	35	14	35	16	8.7
h	90×64	1500×30	600× 8	1650×28	800×29	33	13	36	17	7.8
h	75×64	1650×33	530× 7	1430×25	650×28	39	12	34	15	10.1
h	83×65	1650	700	1900						
h	75×60	1650×30	600	1700×24	750×24	35	13	36	16	11.0
d	90×83	1900×37	2300	1800×26	600×27	29	35	27	9	9.4
d	105×75	2600×34	3500× 7	1650×26	850×27	30	41	19	10	11.2
d	105×75	2900×36	3800×10	1550×24	800×24	32	42	17	9	13.3
d	115×82	3300×38	4000×10	1400×25	1000×25	34	41	14	10	13.3
dd	120×85	4900×36	5000×12	1500×25	950×27	40	40	12	8	17.3
Mean	78	1968×33 ±250	1657× 9	1552×26 ±50	738×27					10.8

[1] The abbreviations used in the tables of the Special section are: *h* high nephron, *hc* cortical nephron, *m* middle high nephron, *d* deep nephron, *dd* deepest nephron, *p.t.* proximal tubule, *t.s.* thin segment, *th.s.* thick segment, *d.t.* distal tubule, *Ind.* index (the ratio of the surface equivalents of the proximal tubule and the capsule, cf. p. 262).

Bracketed figures are not measured but estimated; figures calculated from estimated values are also bracketed.

The dimensions of a number of tubules are given in table 1. Among a number of examined loops there are 78 short loops and 24 long ones. The longest measured nephron nearly reached the apex of the papilla. The mean length of the proximal tubules is 2.0 ± 0.25 mm, which figure is probably slightly too high, as the deep nephrons are somewhat too numerous. For the same reason the mean length of the thin segments is overestimated, but this is probably not the case with the means of the thick segments and the distal tubules. A "mean nephron" thus seems to have about this composition: Proximal tubule 33 %, thin segment 28 %, thick segment 26 %, distal tubule 13 %.

Antechinomys laniger (Gould).

Material. The kidneys of a female in alcohol.

Form. Size: 8.5 × 5 × 4 mm. They are of the same form as those of *Sminthopsis*, but the papilla is a little longer (fig. 4 *C*, p. 271). After maceration the cortex measures 1.0 mm, the outer zone 1.5 mm, of which the outer stripe is 0.3 mm, the inner zone 2.9 mm.

The tubules. These are on the whole similar to the tubules of *Sminthopsis*. The epithelium of Bowman's capsule, however, is thin and transparent everywhere. The thick segment is markedly differentiated into a thicker and a thinner part (respectively 35 μ and 20 μ thick). The thick segment is most often slightly more tortuous than in *Sminthopsis*.

Among a number of examined loops there are 55 short loops and 24 long ones. It is obvious that the thin segment is relatively longer in

Table 2. *Antechinomys laniger*, *tubule dimensions in* μ.

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	70× 60	1800×31	800×10	1730×18	700	36	16	34	14	13.3
h	85× 70	1850×32	1050× 8	2050×21	650×30	33	19	37	12	9.9
h	85× 60	2000×31	1000	2100×20	650×26	35	17	37	12	12.2
h	105× 75	2200×38	1000×10	2100×23	750×30	36	17	35	12	10.6
m	105× 85	2200×33	1100× 9	2450×21	750×32	34	17	38	12	8.1
h	100× 60	2300×30	950× 7	2300×22	600×31	37	15	37	10	11.5
m	110× 85	2500×33		2400×20	680					8.8
m	105× 65	2600×34		2600×24	700×33					13.0
dd	165×120	5000×38	(7000)	2200×20	650×25	(34)	(47)	(15)	(4)	9.6
Mean	89	2494×33	9	2214×21	681×30					10.8

Antechinomys than in *Sminthopsis*, as the long loops are more numerous. As this part is somewhat overestimated in *Sminthopsis*, it would seem that the figures given for the "mean nephron" in that species should apply to this species, too.

Didelphys opossum L.

Material. Several pairs of kidneys in alcohol, one of which has been macerated.

Form. The kidney, which has later been macerated, has the following dimensions: 37 × 19 × 18 mm. The papilla is low (fig. 4 *D*, p. 271). The cortex is 3.5—4 mm thick, after maceration about 5 mm. The corresponding values are, for the outer zone, 5 mm and 6 mm, and for the inner zone 8 mm and 11 mm.

The tubules. Even after prolonged maceration it has hardly been possible to tease the medulla, and in the cortex the tubules are very fragile. The results are therefore fragmentary. The capsule is nearly always oval, with a low transparent epithelium. There is no neck. The proximal tubules are mostly of uniform thickness. There are no cortical nephrons. The thick segment is differentiated into a thicker part in the outer zone and a thinner part in the cortex. The contour of the distal tubule is fairly even. Some proximal tubules have been isolated. Their measurements, in μ, are given below.

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
m	295×200	13500	(16.0)	*d*	280×200	15000×67	17.9
h	310×195	14700×71	17.3	*h*	300×210	15800×76	17.4
h	260×205	15000×63	17.7	*h*	300×200	16500×74	20.4

Macropus giganteus (Zimm.).

Material. One kidney in alcohol.

Form. The dimensions are 82 × 52 × 28 mm. There is a low papilla (Fig 4 *L*). The cortex is 8 mm thick, the outer zone 9 mm, the inner zone 17 mm.

The tubules. After maceration the tubules are very brittle and have shrunk about 10 %. There are no cortical nephrons. The capsule and the proximal tubule present nothing uncommon. The collecting tubules, sometimes at any rate, begin with arcades. It has been possible to prepare only two proximal tubules.

	Capsule	Prox. tubule	Ind.
m	270×190	12000×47	11.0
h	220×220	13000×45	12.1

***Marsupialia*, survey of the form of the kidney.**

All examined *Polyprotodontia* have simple kidneys with a papilla. The latter is long and pointed in *Philander*, *Sminthopsis* and *Antechinomys*, moderately long in *Perameles* and *Dasyurus viverrinus* (Shaw) (fig. 4 *E*, cf. also Gerhardt 1914). In *Didelphys opossum* L. and *Sarcophilus satanicus* Thom. the papilla is low and crest-like (fig. 4 *F*). Owen (1847 a) has found grooves containing blood-vessels on the surface of the kidneys of *Dasyurus viverrinus* (Shaw) and *D. macrourus* Geoff. [= *D. maculatus* (Kerr.)]. Like Gerhardt (1914), I have not been able to find them in *D. viverrinus*, but my material, like that of Gerhardt, is not very well preserved. In *Sarcophilus satanicus* Thom., however, there are distinct grooves. They are relatively deep and divide the kidney surface into several fields (fig. 4 *G*, *H*). Though the kidney thus seems lobated exteriorly, neither the cortex nor the medulla is divided, but the former forms ridges on its inner surface, corresponding to the grooves. Except in *Sarcophilus* the cortico-medullary boundary is even, and, in well-preserved kidneys, marked. The area cribrosa is small and rounded, or oblong, as in *Didelphys* and *Sarcophilus*.

In the *Diprotodontia* there is generally a distinct papilla, also. In *Acrobates pygmaeus* (Shaw) (fig. 4 *I*) it is long and pointed, and somewhat less so in *Petaurus breviceps* Waterh., *Phascolarctus cinereus* (Goldf.), and *Phalangista vulpina* (Meyer) (fig. 4 *K*). In *Macropus giganteus* I have found a very low papilla (fig. 4 *L*), but Gerhardt (1914) states that all kangaroos examined by him possess very large papillae (*Macropus giganteus*, *Halmaturus thetidis* Less., *Thylogale eugenii* Desm.). Judging from Pl. I, fig. 6 (op. cit.) it seems that *Thylogale* has a very low papilla, but from the section of *Macropus* (Pl. I, fig. 7 a) it is evident that Gerhardt's specimen had a more pointed papilla than mine. It is difficult to say whether this is due to individual or perhaps racial differences (Gerhardt's specimen belonged to the smaller race *melanops*), or possibly to differences of age. The last possibility is perhaps the most probable, as the joint thickness of cortex and medulla is the same in both specimens, though mine is much larger (cf. p. 393).

In *Phascolomys wombat* Perron & Lessueur (Hyrtl 1872), *Ph. latifrons* Owen (Gerhardt 1914) and *Ph. mitchelli* Owen there is no papilla, but the area cribrosa lies on a narrow crest (fig. 4 *M*).

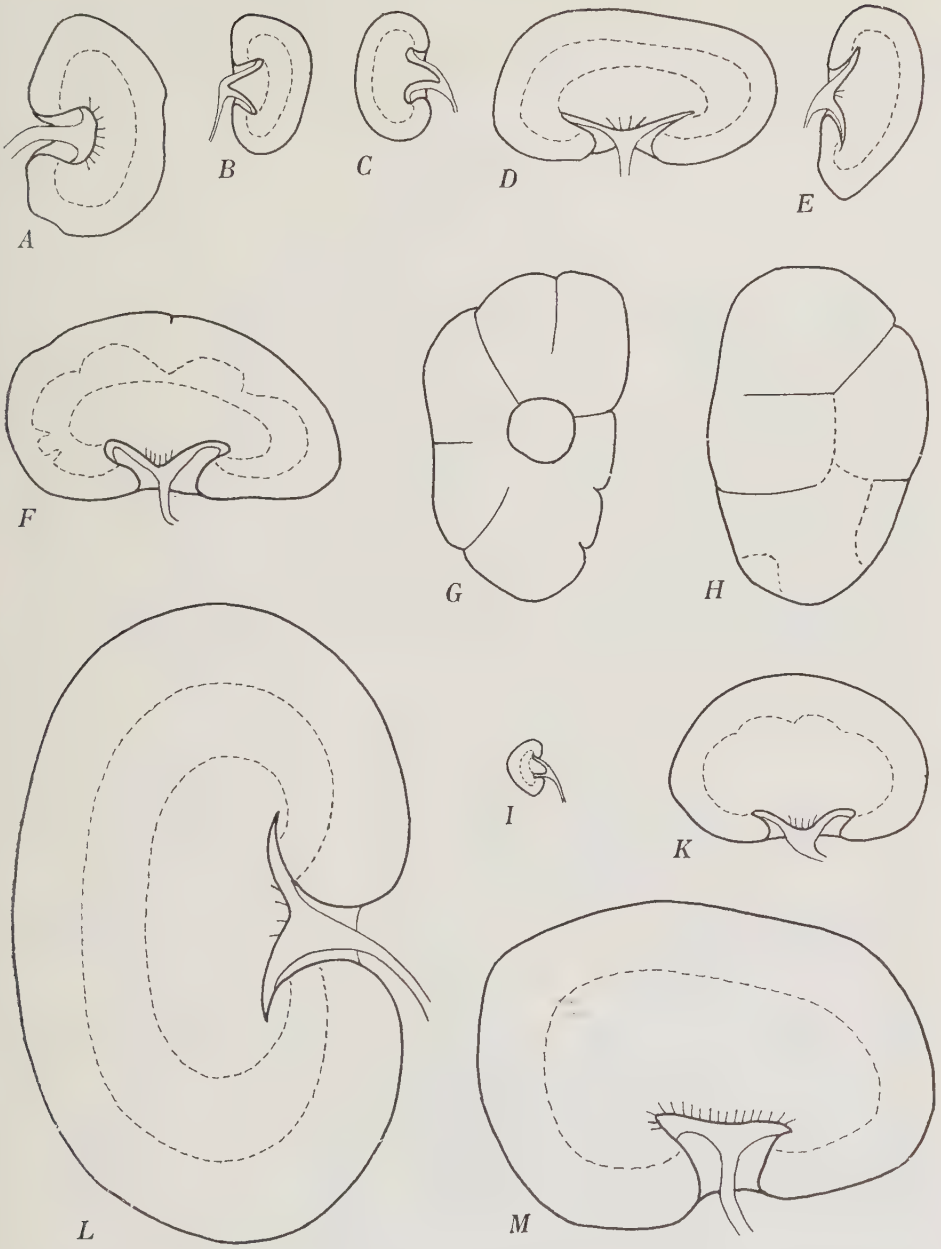


Fig. 4. Kidneys of *Monotremata* and *Marsupialia*. *A Ornithorhynchus anatinus* Shaw. *B Sminthopsis murina* (Waterh.) 2 ×. *C Antechinomys laniger* (Gould) 2 ×. *D Didelphys opossum* L. *E Dasyurus viverrinus* (Shaw). *F, G, H Sarcophilus satanicus* Thom. (*G* ventral, *H* dorsal view). *I Acrobates pygmaeus* (Shaw). *K Phalangista vulpina* (Meyer). *L Macropus giganteus* (Zimm.). *M Phascolomys mitchelli* Owen.

The cortico-medullary boundary is marked and even in the *Diprotodontia*, and the medulla is as a rule distinctly divided into an outer and an inner zone (*Macropus*, *Phalangista*, *Acrobates*, *Phascolarctus*).

Insectivora.

Macroscelides sp.

Material. The kidneys of a specimen in alcohol.

Form. Dimensions 10 × 7 × 5 mm. The long pointed papilla projects into the ureter (fig. 5 *C*, p. 282). Cortex 1.4 mm, outer zone 2.6 mm, inner zone 4 mm thick.

The tubules. These agree with those of the shrews in all essential features (cf. p. 274). The thick segments are mostly wavily tortuous in the outer zone. Out of 109 loops 37 are long ones. After maceration there is a swelling of about 10 %, as compared with the alcohol material. The mean lengths of the proximal tubule and the thick segment in table 3 may be accepted as the true values, as there is no marked deviation of the ratio of long-looped and short-looped nephrons as compared with the true value of this ratio.

Table 3. *Macroscelides sp., tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	130×115	3100×41		3100×36	900					8.5
m	150×110	3200×42		2900×33	750					8.1
h	115×100	3300×44	950×12	3300×34	650	40	12	40	8	12.6
h	140× 95	3300×41	900	2800×31	750×35	43	12	36	10	10.2
h	120×120	3500×43	900×11	3100×35	900×38	42	11	37	11	10.5
h	175×100	3600×45	700×15	3200×38	900×34	43	8	38	11	9.3
m	165×135	4200×45		3900×34	1000×36					8.5
m	150×150	4300×46		3600×32	700×38					8.8
d	150×150	5400×47		4200×35	900×38					11.3
dd	175×150	8100×46	(10000)	3000×30	950×36	(36)	(45)	(14)	(4)	14.2
Mean	135	4200×44 ±490	13	3310×34 ±140	840×36					10.2

Erinaceus europaeus L.

Material. The kidneys of a male.

Form. The weight of one kidney 3.0 gm, its dimensions 24 × 15 × 14 mm. The thickness of the cortex about 2.4 mm, of the outer zone 2.3 mm (outer stripe about 0.4 mm), and of the inner zone 5.6 mm. The pelvis has marked processes, and the papilla is pointed. (fig. 5 *D*, p. 282).

The tubules. The capsule is of the usual shape and structure. Often there is a slight indication of a neck. Occasionally the capsule lies peripheral to the convolute of the proximal tubule, even in the highest nephrons. This means that some of the capsules are situated immediately beneath the surface of the kidney, and there is no marked cortex corticis.

Normally, the short loops turn in the thick segment at various levels; the loops of the highest nephrons turn about 0.6 mm above the zone boundary. The thick segment is differentiated into a thicker and a thinner part. The distal tubule also consists of two parts. The first of these is considerably thicker than the thick segment, and its epithelium contains a great number of small refractive droplets, so that this segment is relatively opaque. The distal tubule then diminishes and becomes more transparent; thus the second part has the structure normally characterizing this segment. The transition is gradual, as is the transition into the initial collecting tubule, which has as usual a low transparent epithelium.

Table 4. *Erinaceus europaeus, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
d		4900								
h	142×113	4950×49								15.1
h	135×130	5150×47								13.8
h				4500×25	1500×42					
h	135×120	5200×50	1650	4350	1500×39	41	13	34	12	16.0
h	140×120	5600×48	1550×10	4450×28	2200×36	41	11	32	16	16.0
m	170×150	5700×52	2800× 9	4450×30	1730×40	39	19	30	12	11.6
m	165×120	5850×50	1850×10	4280×26	2180×38	41	13	30	15	14.8
d		6000								
d		6100×49								
d		6980×50		2500×31						
Mean	137	5643×49 ±200	10	4105×28 ±140	1822×39					14.6

The collecting tubules are thin, and have the same appearance as the preceding segment. The peripheral junctions are mostly direct, but sometimes there are small arcades, or the initial collecting tubules unite in pairs (cf. fig. 11 nr *12*, p. 319). The initial collecting tubules are generally long when they join the collecting tubules directly, but short when the nephrons join arcades, in which case they may be absent altogether.

After maceration there is a swelling of slightly more than 10 %. The long loops constitute 39 ± 4.3 % of the total number. Taking into account the swelling, the mean length of the proximal tubules is 5.0 mm. It would seem that one of the deepest nephrons ought to have the following dimensions: Proximal tubule 6.3 mm, 27 %, thin segment 12 mm, 52 %, thick segment 2.3 mm, 10 %, distal tubule 2.4 mm, 10 %. It must, however, be taken into consideration that the proximal tubule is undoubtedly underestimated, as no special search has been made for the longest tubules.

Sorex araneus L.

Material. Several specimens have been examined with regard to the form, weight, and dimensions of their kidneys. A more thorough investigation after maceration has been made of a young male (born the year of its capture) and a female (more than a year old).

Form. The kidneys are covered by the peritoneum dorsally as well as ventrally, and are thus relatively loosely fastened to the dorsal abdominal wall. They are of the common bean shape (fig. 5 *A*, p. 282). The papilla is distinct but does not project very much into the pelvis. The latter has processes. In young individuals (total weight 6—8 gm) the total kidney weight is most often 0.13—0.15 gm, and the dimensions of a kidney about 7 × 5 × 3.5 mm. In older animals (body weight 10—14 gm) the kidney weight is 0.18—0.35 gm with measurements up to 9×6×4 mm. The cortex is about 0.9 mm in the former, and up to 1.2 mm in the latter. The corresponding values of the outer zone are, 1.0 and 1.1, and of the inner zone, 1.5—2.0 and about 2.0.

The tubules. Bowman's capsule has a thin, transparent epithelium. The proximal tubule is usually only slightly coiled, especially in the high nephrons. The bends are gentle and smooth. The last segment is, normally, more transparent. The thin segment has the usual low epithelium and the thick segment is, at least in the higher nephrons, differentiated into a thicker and a thinner part. The short loops turn in the thick segment at different levels in the inner stripe of the outer zone. The loops of the highest nephrons turn about 0.3 mm from the zone boundary. The outer stripe is sharply demarcated microscopically. The distal

tubule is markedly thicker than the last part of the thick segment, and its contour is even, without any projections. The transition to the initial collecting tubule is gradual. The latter is thinner and more transparent. The peripheral junctions are, normally, direct ones, and the first central junctions occur in the most peripheral part of the inner zone. The collecting tubules are rather thin, even in the central parts of the medulla.

Table 5 a refers to an old female, kidney weight 0.35 gm. The percentage of long loops is 12 ± 2.3.

As the low nephrons are somewhat too numerous, the mean length of the proximal tubule will be lower than that given in the table, about 2.2 mm. The mean length of the thin segment is estimated at 0.9 mm, that of the thick segment at 1.7 mm and that of the distal tubule at 0.64 mm.

Table 5 a. *Sorex araneus, old female, tubule dimensions in* μ.

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	75×60	1850×40	550×8	1600×22	630×32	40	12	35	14	16.4
h	60×60	2050×38	530×8	1730×22	650×30	41	11	35	13	21.6
h	82×64	2060×40	640×9	1850×22						15.7
h	75×60	2150×41	650×9	1800×21	600×31	41	13	35	12	19.6
h	83×56	2180×40	520×8	1600×21	670×32	44	10	32	13	18.8
m	90×68	2200×41	750×9	1950×24	620×31	40	14	35	11	14.7
d	83×76	2250×38	2400×7	1450×22	600×30	34	36	22	9	13.6
m	86×70	2330×40	1800×8	1780×23	630×30	36	28	27	10	15.5
d	90×75	2500×41	2600×9	1280×24	700×36	35	37	18	10	15.2
m	97×78	2600×42	2450×9	1800×22	600×31	35	33	24	8	14.4
d	90×68	2800×40	3000×8	1430	600×35	36	38	18	8	18.3
d	90×63	2800×41	3300×9	1330×24	680×35	35	41	16	8	20.2
d	108×75	2850×41	2700×8	1680×21	675×31	36	34	21	9	14.4
d	105×65	3300×43	3600	1650×23	840×36	35	38	18	9	20.8
d	94×75	3450×42	3500×9	1200×26	825×34	38	39	13	9	20.6
d			4000×8	1580×26	900×34					
dd	94×86	4880×39								23.5
dd		(5000)	(4800)	(1100)	(1000)	(42)	(40)	(9)	(8)	
Mean	78	2640×40	8	1607×23	676×32					17.7

Table 5 b. *Sorex araneus, young male, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
h	68×61	1350×31	10.2	*m*	75×63	1740×34	12.5
h	70×60	1510×32	11.5	*m*	83×74	1880×34	10.4
h	72×64	1530×32	10.6	*d*	86×75	1950×35	10.6
h	75×53	1540×31	12.0	*m*	79×57	2020×31	13.9
m	80×57	1730×32	12.1	*d*	96×84	2940×34	12.4

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	71×56	1390×32	370×6	1430	525×23	37	10	38	14	11.2
h	68×53	1500×31	350×5	1350×20	670×23	39	9	35	17	12.9
h	75×66	1580×33	450×5	1440×21	530×24	40	11	36	13	10.5
m		1870×32	1850×6	1170×21	750×24	33	33	21	13	
d	95×84	2330×33		920×23	840×30					9.6
dd		(3000)	(4200)	(1000)	(1000)	(31)	(46)	(11)	(11)	
Mean	71	1791×32.5 ±110	6	1262×21	25					11.5

Table 5 b refers to a young male. The ratio of long and short loops is 13: 42. The mean length of the proximal tubule may be estimated at 1.6 mm.

Sorex minutus L.

Material. The kidneys of an old male.

Form. The agreement with *S. araneus* is very close. Kidney weight 0.075 gm. Dimensions: $5.5 \times 3.5 \times 3$ and $5 \times 3.5 \times 3.5$ mm. Cortex 0.6 mm thick, outer zone 0.8 mm, inner zone 1.1 mm.

The tubules. The tubules, also, agree in essentials with those of *S. araneus* (Pl. 3, fig. *1*). The proximal tubules are still less tortuous than those of *S. araneus*, but the loops and distal tubules show no deviations from the corresponding parts of the common shrew. The peripheral junctions of the collecting tubules are nearly always direct. In the deepest nephrons the initial collecting tubule often joins a collecting tubule in the medulla, even in the inner zone, where, normally, there are only central junctions. Such an initial collecting tubule may well be looked upon as a collecting tubule with only one nephron, and the

Table 6. *Sorex minutus, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
h	45×40	820×24	10.9	*h*	55×45	900		*m*	48×44	1000	
h	38×37	820×25	14.6	*h*	45×40	900×26	13.0	*m*	56×52	1050×28	10.1
h	60×38	825×27	9.8	*h*	57×48	940		*m*	56×50	1150×26	10.7
h	45×40	840×26	12.1	*m*	55×38	950×26	11.8	*m*	68×45	1200×26	10.2
h	54×35	860×25	11.4	*m*	52×40	960		*d*	68×48	1275×27	10.5
h	52×35	880×27	13.1	*h*	50×42	970×24	11.1	*d*	68×50	1350×25	9.9
m	62×34	900×26	11.1	*m*	56×32	1000×26	14.5	*d*	72×52	1500×27	10.8

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
a[1]	56×45	1070×24	310×4	830×18	460×20	40	12	31	17	
a	49×36	1100×23	320×5	850×18	380×19	42	12	32	14	
a	54×42	1130×23	285×4	810×17	450×19	42	11	30	17	
a	52×39	1140×24	260×4	790×18	450×20	43	10	30	17	
a	47×39	1180×24	340×4	850×21						
a	56×40	1350×29	375×4	900×19	600×22	42	12	28	19	
h	53×40	860×26	340	850						10.5
h	48×40	950×26	320×5	800	300	40	14	34	13	12.9
m	55×35	1020×27	340×6	880×14	350×18	39	13	34	14	14.3
d	50×45	1100×27	550×6	1050×17	350×22	36	18	34	11	13.2
dd		(1800)	(2600)	(900)	(800)	(30)	(43)	(15)	(13)	
Mean[1]	48	1001×26 ±35	6	895×16	333×20					11.7

differences between central and peripheral junctions becomes less distinct in this species.

Table 6 includes nephrons that have been mounted in Canada balsam after staining with borax carmine.[1] The percentage of long loops is 16 ± 3.1.

[1] The nephrons mounted in Canada balsam are distinguished with *a* and are not included in the mean.

Table 7. *Neomys fodiens, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t	
h	58×58	1100×27								8.8
h	50×48	1150×25	640×4	1150	320×24	35	20	35	10	12.0
h	64×53	1150×26	300	900×15	375	42	11	33	14	8.8
h	72×52	1280×28								9.6
h	72×42	1280×27	340×5	1000×18	640×23	39	10	31	20	11.4
h	68×68	1300×29	450×5	1200×16	430×25	38	13	36	13	8.2
h	72×48	1300×26	360×4	1150×19	480×22	40	11	35	14	9.8
h	90×50	1350	350	1100	350	40	10	33	17	
h	58×55	1350×28	400×5	1100×20	550×23	40	12	32	16	11.8
m	68×64	1350×29	700	1150						9.0
h	60×45	1400×26	350×5	1100×18	480×22	42	11	33	14	13.5
m	74×64	1430×29	680×5	1050×19						8.8
m	88×50	1450×28	500	1200×18	650×23	38	13	32	17	9.2
h	85×50	1450×26	400	1100×18	620×22	41	11	33	17	8.9
h	85×50	1450	500	1200	650	38	13	32	17	
h	72×56	1450×27	400	1300×20	600×22	39	11	35	15	9.7
h	70×70	1450	350	1200	650	40	10	33	17	
m	68×62	1500×30	640×6	1150×18	400×28	41	17	31	11	10.7
h	80×65	1500×27	475×5	1300×18	750×22	37	12	32	19	7.8
m	85×65	1500	1000	1300	600	34	23	30	13	
d	80×56	1500×26	2000	650×19	800×23	30	40	13	17	8.7
h	68×60	1500×29	550×5	1250×19	480×25	40	15	33	12	10.7
m	72×64	1600×29								10.1
h	88×55	1600								
m	83×65	1600×30	1650×6	1130×19	450×24	32	33	23	12	8.9
h	68×60	1600×28	580×6	1230×17	450×24	41	15	32	12	11.0
h	80×58	1600×30	410×5	1280×18	800×24	39	10	31	20	10.3
m	64×64	1680×29								11.9
h	88×55	1680×30								10.4
d	88×56	1700×31	1500×6	1000×20	480×24	36	32	21	11	10.7
m	90×65	1700×30	1500×6	1200×18	550×22	34	30	24	12	8.7
d	80×75	1730×29	1900×8	600×18	600×19	36	39	12	13	8.4
m	80×64	1750								
m	100×71	1750×30	2270×7	1300×13	540×20	30	39	22	9	7.4
m	82×75	1750×29	1350	1200						8.3

Table 7 (Cont.)

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
d	72×68	1760×30	1700×5	1100×22	400×26	35	34	22	8	10.8
d	80×50	1760×31								13.6
d	85×70	1760×28	1800×6	1100×20	480×24	34	35	21	10	8.3
m	90×72	1760×30	1600×7	1300×20	700×23	33	30	24	13	8.1
d	79×71	1800×29	2000×6	1130×18	450×27	33	37	21	9	9.3
d	88×65	1800×29	1800×6	1040×19	600×24	34	34	20	12	9.1
m	80×70	1850×30	1700	1250	320	36	33	24	6	9.9
m	80×72	1850								
d	85×80	1900×31	2100×6	1100×18	600×23	33	37	19	11	8.7
m	104×80	2000×29	2300×6	1300×16	800×24	31	36	20	13	7.0
d	112×72	2000×30	2300×7	1050×18	650×23	33	38	18	11	7.4
d	100×95	2000×31	2100×7	1200×18	550×25	34	36	21	9	6.5
d	80×60	2000×31	2000×5	1100×20	400×23	36	36	20	7	12.9
d	88×84	2000×30								8.1
d	84×75	2050×30	2000×7	1050×19	500×26	37	36	19	8	9.8
d	96×60	2100×30	2800×6	960×18	800×24	32	42	14	12	10.9
d	75×65	2150×30	2200×8	900×20	380×24	38	39	16	7	13.2
d		2200×30	2900×7	1000×21						
d	104×96	2480×32								7.9
d	95×80	3050×32		900×19	500×26					12.8
d	105×90	3100×30	3500×8	960×19	800×24	37	42	11	10	9.8
dd		(3300)	(4000)	(900)	(800)	(37)	(44)	(10)	(9)	
Mean	72	1702×29	6	1105×19	552×24					9.66

Neomys fodiens Schreb.

Material. The kidneys of a young male (body weight 8.8 gm).

Form. The kidneys are of the same form as those of *Sorex araneus*. Their weight is 0.19 gm. The dimensions of the right kidney are $6.5 \times 5 \times 3.8$ mm. The cortex measures 0.7 mm, the outer zone 0.9, the inner zone 1.6 mm.

The tubules. These agree very closely with those of *S. araneus*. 21 ± 3.2 % of the loops are long. The mean length of the proximal tubules is about 1.5 mm (mean of high nephrons 1.4 ± 0.035 mm, of nephrons with long loops 1.9 ± 0.04 mm). The means of the other segments are: Thin segment 0.8 mm, thick segment 1.15 mm, distal tubule 0.55 mm.

Pachyura etrusca Savi.

Material. The kidneys of a specimen in alcohol.

Form. Exteriorly, the kidneys are of the same shape as those of the other shrews, but the dimensions are, of course, smaller: 4.3 × 2.8 × 2.3 mm. The papilla, however, is relatively much longer in this species, and projects into the beginning of the ureter (fig. 5 *B*, p. 282). The cortex is 0.5 mm thick, the outer zone 0.75 mm, the inner zone 1.3 mm.

The tubules. I have not been able to detect any differences as compared with *Sorex minutus*.

91 short and 20 long loops have been counted.

The tabulated nephrons (except the deepest one) are all prepared from the same small piece, and may be considered representative of the average composition of the kidney.

Table 8. *Pachyura etrusca, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	49×40	830×26	290×7	800×20	350×19	37	13	35	15	11.0
h	45×40	870×23	270×7	840×18	350×20	37	12	36	15	11.1
h	53×38	900×26	450×5	860×20	350×20	35	18	34	14	11.6
h	50×45	940×25	320×6	900×19	380×20	37	13	35	15	10.4
h	44×39	950×23	430×5	880×20	400×18	36	16	33	15	12.7
h	50×41	970×25	370×6	950×19	380×20	36	14	36	14	11.8
m	54×50	1200×27	600×7	1070×19	450×19	36	18	32	14	12.0
m	52×50	1250×26	500×7	1100×20	410×20	38	15	34	13	12.5
m	49×48	1450×29	1900×8	1200×19	370×20	29	39	24	8	17.9
d	64×45	1580×30	2400×6	1200×19	470×19	28	42	21	8	17.6
dd	71×60	3050×31	(3000)	1150×20	600×19	(39)	(38)	(15)	(8)	22.2
Mean[1]	47	1094×26 ±83	753×6 ±240	980×19 ±48	391×20					12.9

Desmana moschata Pall.

Material. One pair of kidneys in alcohol.

Form. Dimensions: 16 × 11 × 7.5 mm. Cortex 2.2 mm thick, outer zone 2.3 mm, inner zone 2.0 mm. The small area cribrosa is situated on

[1] Not including the deepest nephron.

a small, short crest, which projects a little way into the pelvis (fig. 5 *F*, p. 282), which has processess.

The tubules. The proximal tubules pass into the thin segment at slightly different levels, the highest at the cortico-medullary boundary. The thin segment is short in the highest nephrons, and the loops of the latter turn only a short distance central to the stripe boundary. There are a few long loops, but their frequency has not been estimated. They probably form about 5 % of the total number. The thick segment is differentiated into a thicker and a thinner part.

Hyrtl (1872) states that *Desmana* has a distinct papilla.

Table 9. *Desmana moschata, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
h	75×63	2650×24	11.1	*h*	75×70	3150×23	13.8
h	75×70	2800×23	12.3	*m*	80×75	3200×25	13.3
m	70×65	2800×22	13.5	*h*	82×70	3400×23	13.6
h	75×60	3000×24	16.0	*d*	80×80	3600×24	13.5
m	78×70	3100×23	13.1	*d*	100×85	4100×23	11.1
				Mean	75	3180×23 ±140	13.4

Insectivora, survey of the form of the kidney.

All insectivores hitherto investigated have simple kidneys. Nearly all of them display a distinct, usually pointed papilla. This is true of *Tupaia* (fig. 5 *E*), *Ptilocercus* (Le Gros Clark 1926), *Macroscelides*, *Centetes* (Dobson 1882, Gerhardt 1914), *Gymnura* (Dobson), *Erinaceus* (Gerhardt 1914, Hyrtl 1872, cf. also Cuvier 1840), *Sorex*, *Neomys*, *Pachyura*, *Talpa* (Gerhardt 1914). *Desmana*, cf. above.

In all kidneys investigated in this respect the pelvis has distinct processes, and the medulla is differentiated into an outer and an inner zone.

Chiroptera.

Pteropus edulis Geoffr.

Material. One pair of kidneys in alcohol.

Form. Dimensions: 20 × 13 × 11 mm. The kidneys are bean-shaped and the pelvis has distinct processes; there is a small pointed papilla (fig. 5 *G*, p. 282). The boundary between cortex and medulla is somewhat indistinct, as there are a great number of relatively thick medullary

Fig. 5. Kidneys and tubules of *Insectivora* and *Chiroptera*. *A Sorex araneus* L. 4 ×. *B Pachyura etrusca* Savi. 4 ×. *C Macroscelides sp.* 2 ×. *D Erinaceus europaeus* L. *E Tupaia sp.* *F Desmana moschata* L. *G Pteropus edulis* Geoffr. *H Vespertilio murinus* L. 2 ×. *I, K, L, M Pipistrellus nilssoni* Keys. & Blasius. *I* high proximal tubule. *K* deep proximal tubule. *L* distal part of nephron. *d.t* distal tubule, *i.c.t* initial collecting tubule, *th.s* thick segment, *t.s* thin segment. *M* portion of the outer zone. *p.r* pars recta, *th.s.l* thick segment of long loop, *th.s.s* thick segment of short loop. *I, K, L* 100 ×, *M* about 70 ×.

rays projecting into the cortex. The latter is about 2.7 mm thick, and the medulla, which is not divided into zones, is about 5.3 mm thick, including the outer stripe, which is about 2 mm.

The tubules. There are a great many cortical nephrons; on the other hand there are no typical long loops. The proximal tubules all have well-developed partes rectae that end at very different levels, from the inner boundary of the outer stripe to the outer zones of the cortex. In exceptional cases the thin segment may be absent, but most cortical nephrons have thin segments. All examined loops turn within the thick segment, but it is possible that the deepest nephrons are an exception to this rule. Fragments of very low loops showed the bend at the transition between thin and thick segment, or occasionally within the thin segment. The thick segment is differentiated into a thicker and a thinner part. This differentiation is very distinct in deep neprons, but is often absent in the cortical nephrons. There is seldom an initial collecting tubule. The collecting tubules are typical arcades and are usually joined by a fairly large number of nephrons. They are also extraordinarily thick, about 0.1 mm even in the cortex.

It may be added that a kidney of *Pteropus medius* Temm. shows the same structure, but the cortex is a little thicker as compared with the medulla.

Table 10. *Pteropus edulis, tubule dimensions in* μ.

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
hc	85× 65	1950×34	0	675×17	750×30	58	0	20	22	12.0
h	82× 75	2600×35	200× 6	950×17	700×24	58	4	21	16	14.8
h	90× 70	2900×34								15.7
m	100× 90	3500×42	550×11	2200×20	600×32	51	8	32	9	16.3
m	105× 90	3900×40	500× 8	1800×20						16.5
d	145×125	4900×52	2700×10	4800×23	1200×45	36	20	35	9	14.1
d	135×115	5200×50	2500×10	4500×26	1100×40	39	19	34	8	16.7
dd	160×130	5500×56	3500×10	5500×25	1100×42	35	22	35	7	14.8
Mean	104	3806×43	1421× 9	2918×21	908×36					15.1

Pipistrellus nilssoni Keys. & Blasius.

Material. The kidneys of a young specimen.

Form. The weight of the kidneys is 0.12 gm and their dimensions are $7 \times 5 \times 3.5$ mm. The papilla is pointed and the pelvis has distinct

Table 11. *Pipistrellus nilssoni, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h		1070	350	1250	530	33	11	39	17	
h	100× 80	1100×30		1400×27	650×29					4.1
h		1200×32		1390×24	700					
h	87× 77	1200×31	650×12	1450×28	550×30	31	17	38	14	5.6
m	102× 86	1250×28	750×10	1400×26	650×31	31	19	35	16	3.4
m	92× 74	1300×30	1100× 8	1300×21	550×23	31	26	31	13	5.7
m	107× 83	1500×32	750×10	1500×29	900×30	32	16	32	19	5.4
h		1550×34	750× 9	1600×28	1000×30	32	15	33	20	
h		1600×31	700× 8	1500×29	800×29	35	15	33	17	
m	120× 93	1600×45	2100× 9	1700×27	750×32	26	34	28	12	6.5
m	140× 80	2000×36		1850×30	800×33					6.4
d	130×130	2800×45		1700×33	1000×28					7.5
d	140×110	2800×37								6.7
d	120×115	3300×35								8.4
d	156×137	4000×44								8.2
dd	160×140	4550×48	(6000)	1490×30	(1000)	(35)	(46)	(12)	(8)	9.8
Mean	111	2051×36 ±270	9	1502×28 ±48	740×30					6.5

processes. The demarcation of the cortex is distinct, and the thickness of the layers is: Cortex 0.85 mm, outer zone 1.3 mm, inner zone 2.8 mm. After maceration an inner and an outer stripe can be seen, the latter about 0.15 mm thick.

The tubules. At times the epithelium of the capsule is more opaque at the beginning of the proximal tubule. There is no neck. The proximal tubules are in the main evenly bent with very few loops (fig. 5 *I*, p. 282), but the central proximal tubules, which are relatively very long, consist of some long loops parallel to the cortico-medullary boundary, and a very short pars recta (fig. 5 *K*). The last part of the proximal tubule is mostly somewhat thinner and less transparent than the main part. The short loops turn within the thick segment, which is differentiated into a thicker and a slightly thinner part (fig. 5 *L*), except in the deepest nephrons. The short loops turn at varying levels (fig. 5 *M*). Normally, the distal tubule has a smooth surface. The initial collecting tubule is occasionally absent. In most cases three or four nephrons join each

collecting tubule in the cortex and the junctions are, normally, direct. The first central junction is most often situated at the zone boundary.

The long loops constitute 25 ± 3.1 % of the total number. The mean length of the tabulated proximal tubules is almost certainly too high, as there are relatively too many deep nephrons measured. The mean length of the proximal tubules of nephrons with short loops is 1.39 mm, and of such as are connected with long loops 2.96 mm. Thus the true mean ought to be about 1.8 mm. The means of the table may be accepted as mean lengths for the thick segments and distal tubules.

Vespertilio murinus L.

Material. The kidneys of a young female and one pair of kidneys in alcohol.

Form. The form is much the same as in *Pipistrellus*, but the papilla is somewhat longer and projects into the ureter (fig. 5 *H*, p. 282). Weight of the fresh kidneys 0.11 gm, dimensions of the same: $7 \times 4.5 \times 3.5$ mm; of one kidney in alcohol $7.2 \times 4.9 \times 4.6$ mm. Cortex 0.9 mm, outer zone 1.3 mm, inner zone 2.9 mm thick in the latter kidney.

The tubules. The agreement with the tubules of *Pipistrellus* is very close. However, the epithelium of the capsule is always low and transparent. It is not possible, as in *Pipistrellus*, to distinguish any structurally different parts of the proximal tubule.

The mean of table 12 a (from a fresh kidney) may be accepted as the mean length of the proximal tubules, since the relation between long and short loops is about the same as in the kidney. In the fresh specimen the long loops constitute 27 ± 3.8 % of the total number and in the alcohol specimen the percentage of long loops is 36 ± 3.9.

In the alcohol specimen 8 further proximal tubules have been measured in addition to the tubules tabulated in table 12 b, as also 17 thick segments. The mean length of the proximal tubules is 1.77 ± 0.05 mm and that of the thick segments 1.85 ± 0.04 mm. The mean length of the distal tubules is about 0.8 mm. The thin segment is 0.6—0.9 mm long in short-looped nephrons, and in long-looped nephrons it is 1—9 mm, on an average probably about 3 mm in the latter. Thus, the mean length of the thin segment may be estimated at about 1.5 mm.

Chiroptera, survey of the form of the kidney.

The kidneys of all *Chiroptera* hitherto examined are simple, with smooth surfaces. As far as I know the following authors have contributed to our knowledge of this subject: Hyrtl (1872) (*Pteropus kerau-*

Table 12 a. *Vespertilio murinus, tubule dimensions in μ.*

Capsule	Prox. tubule	Ind.	Capsule	Prox. tubule	Ind.	Capsule	Prox. tubule	Ind.
106×66	1320×33	6.2	106×82	1600×40	7.4	133× 74	1850×40	7.5
105×75	1400×35	6.2	96×82	1700×37	8.0	114× 90	1860×37	6.7
109×85	1400×35	5.3	102×80	1700×36	7.5	123× 98	1890×40	6.3
105×70	1400×34	6.5	132×80	1700×45	7.2	130× 80	2010×40	7.7
100×69	1460×38	8.0	106×83	1700×33	6.4	110× 83	2100×40	7.2
88×85	1530×38	7.8	95×72	1800×37	9.7	145×115	2350×46	6.5
95×82	1580×31	6.3	119×90	1800×40	6.7	167×138	3300×48	6.9
101×82	1600×40	7.7						

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	90×70	1380×29	600× 7	1380×20	600×19	35	15	35	15	6.4
h	93×70	1400×30	440× 8	1370×21	750	35	11	35	19	6.5
h	104×88	1600×38	520× 7	1580×19	790×23	36	12	35	18	6.6
h	103×90	1750×30	700×10	1600	750	36	15	33	16	5.7
m	158×85	1930×39	1430×10	1910×25	670×25	32	24	32	11	5.6
d	160×98	2250×39	1600× 7	1700×22	900×19	35	25	26	14	5.6
dd		(3500)	(5500)	(1200)	(1000)	(32)	(50)	(11)	(9)	
Mean	99	1763×37 ±75	8	1590×21	743×22					6.9

Table 12 b. *Vespertilio murinus, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
h	95×65	1430×30	6.9	*h*	98×60	1650×38	10.7
m	95×70	1520×36	9.7	*m*	90×90	1800×40	8.9
m	90×75	1560×35	8.1	*d*	105×75	1880×40	9.5
h	90×75	1580×33	7.7	*d*	110×85	2100×45	10.1
h	80×75	1600×32	8.5	*d*	95×90	2150×41	10.3
				Mean	85	1727×37	9.0

denii Quoy & Gaim., *P. edwardsii* Dobs.), Gerhardt (1914) (*Pteropus edulis* Geoffr.), Inouye (1931) (*Pteropus pselaphon* Sav.), and especially Robin (1881), who examined 46 species from all groups of this order.

The papilla is not very long in the *Megachiroptera*, but in several *Microchiroptera* it is very long and projects into the ureter. According to Robin this is especially the case in *Emballonura nigrescens* Gray, and to a less degree in some other forms.

In the *Microchiroptera* which I have examined, the medulla is divided into inner zone and outer zone, but this is not the case in the two species of *Pteropus*. It seems probable that the few examined species are representative of their suborders in this respect.

Xenarthra and Pholidota.

Survey of the form of the kidney.

The kidneys of *Dasypus villosus* Desm. (Gerhardt 1914) and *Dasypus sexcinctus* L. (fig. 6 *A*) have a distinct papilla, more prominent in the former species. The area cribrosa is small, situated on the apex of the papilla. *Dasypus novemcinctus* L. (Hyrtl 1872) also has a papilla, and the pelvis has processes.

Bradypus tridactylus L. (Hyrtl 1872, Gerhardt 1914) and *Choloepus didactylus* L. (Hyrtl 1872) have a simple pelvis without processes. This is also the case in a kidney of a *Bradypus sp.*, which I have examined. The papilla is crest-like and the area cribrosa oblong (fig. 6 *B*).

In *Myrmecophaga* (Hyrtl 1872) and *Cyclopes* the pelvis has processes. In the latter there is a distinct papilla (fig. 6 *C*).

Manis javanica Desm. has round, flattened kidneys with a small, obtuse papilla (fig. 6 *D*).

Rapp (1852) states that all "*Edentata*" have simple, smooth kidneys.

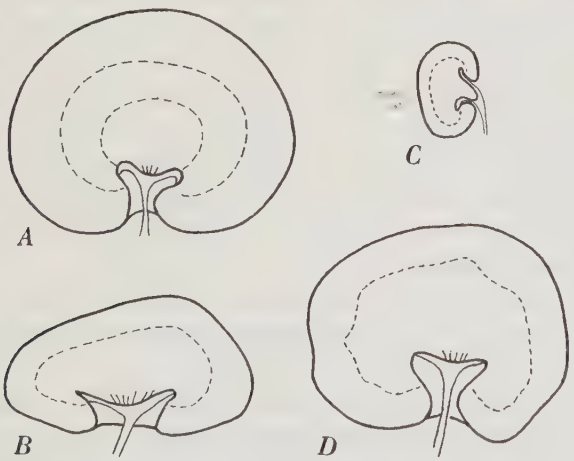


Fig. 6. Kidneys of *A Dasypus sexcinctus* L., *B Bradypus sp.*, *C Cyclopes didactylus* L., *D Manis javanica* Desm.

Rodentia.

Oryctolagus cuniculus (L.).

Material. Several kidneys of the domesticated form. Several of the specimens belonged to the same family (Swedish white country breed).

Form. Dimensions:

	Weight, one kidney, gm	Dimensions, mm	Thickness of		
			cortex, mm	out. z. mm	inn. z. mm
Young, 7 days old	0.58	14.5× 9 × 8.5	2.0	5.5	
Young, 3 weeks	4.1	27 ×17 ×16	2.5	2.0	9
Young, 8 weeks	6.8	31 ×23 ×18.5	3.3	2.9	10
Young, 2 months	7.2	32 ×24 ×15	3.2	3.0	10
Male, 6 months	9.0	35 ×24.5×18.5	4.8	4.3	9
Male, 8 months	10.5		4.5	4.3	9
Male, 10 months	11	36.5×26.5×21	5	5	9.5
Old female	17	44 ×34 ×25	5.5	5.5	10

These specimens form a series from the same family.

The cortico-medullary boundary is distinct, like the zone boundary, except in very young specimens, where the latter is not visible to the naked eye. In most cases the stripe boundary also is visible. The pelvis has processes and the papilla is well developed, with the small area cribrosa on its apex (fig. 7 *A*, p. 295).

The tubules. The capsule is, normally, almost round, and somewhat irregular. In some kidneys almost every nephron has a distinct neck, but in others no trace of a neck is to be found. The proximal tubule in most cases is somewhat thicker in its distal part, but sometimes all proximal tubules in a kidney are thickest in the middle part. More constant than these differences is a slight differentiation of the terminal part of the proximal tubule, which has in most cases a more transparent epithelium. Here the cell boundaries are often visible, which is not the case in the other parts.

The pars recta is short in the deepest nephrons, but always distinct. In the "Old female" it is very tortuous, like all parts of the nephron (Pl. 1, fig. *4*).

The transition into the thin segment sometimes occurs at slightly varying levels. The latter is very transparent.

The thick segment has a thicker and a thinner part. This differentiation is very marked in the high nephrons, where the thin part is long,

very thin, and transparent. In the deepest nephrons the thinner part is short and resembles the thicker part much more. The short loops normally turn in the inner part of the outer zone only. An exception to this is the "Male, 6 months" which has some cortical nephrons and where some loops turn in the outer stripe. The short loops most often turn where the thin segment passes into the thick segment.

In some specimens the first part of the distal tubule shows the same structure as the thinner part of the thick segment (Pl. 3, fig. *2*), but normally there is no intercalated segment. In the latter case the transition into the distal tubule is very marked. The contour of the distal tubule is even in the younger individuals, but in the older ones it has often some small projections, which make the contour irregular.

The highest nephrons generally have initial collecting tubules, but in nephrons joining arcades they are, as a rule, absent.

The collecting tubules are normally arcades with a small peripheral branch (fig. 7 *B*, p. 295). The ascending part of the arcade never lies in the medullary rays, where the descending part is always situated. This has been confirmed in each of several kidneys examined in respect of this. This is also true of other kidneys possessing well-developed arcades.

When distal tubules join the ascending part of the arcade, the structure of the arcade, immediately above the junction, may often be apparently identical with that of the distal tubule. Such segments may then alternate with segments of the structure typical of the collecting tubules. The collecting tubules are slender, especially in the cortex and the outer zone (25—35 μ). The central junctions occur in the inner zone, but sometimes also in the inner parts of the outer zone.

The dimensions of some nephrons are tabulated in table 13.

The mean dimensions of the proximal tubules of some other kidneys are:

Young, kidney weight	5.75 gm	8.5×0.047	mm,	index	17
Young, kidney weight	7.25 »	8.9×0.053	»	»	16
Young		9.1×0.052	»	»	19
Young, kidney weight	9.15 »	10.2	»	»	19
Young, kidney weight	12 »	9	»	»	15

These rabbits belong to various races, and the means have been calculated from 9—28 tubules.

The long loops have been counted in the following specimens: "Young, 2 months old" 44 ± 3.6 %, "Male, 6 months" 44 ± 4.4 %, "Male, 8 months" 43 ± 3.4 %, "Male, 10 months" 48 ± 2.7 %, "Female, 10 months" 46 ± 4.2 %.

The mean lengths of the segments have been estimated in the two last-mentioned specimens, which may be considered full-grown. The figures are, respectively: Proximal tubule 16.2 ± 0.40 and 16.7 ± 0.29 mm, thin

Table 13 a. *Rabbit, young, 7 days old, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
h	83× 60	1280×27	6.9
h	95× 68	1650×31	7.9
m	95× 84	2180×36	9.8
d	111×100	2800×40	10.1
d	128× 98	3000×38	9.1
d	130×105	3150×39	9.0
d	120×113	3150×41	9.5
d	160×120	3450×43	7.7
d	158×112	3700×45	9.4
d		4150×41	
Mean[1]	97	2641×37 ±210	10.2

Table 13 b. *Rabbit, young, 4 weeks old, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
m	115× 80	4500×38	18.6
h	120× 90	4650×39	16.8
h	100× 90	4800×40	21.3
h		5250×38	
m	130× 85	5300×40	19.2
m	105×100	5400×37	19.0
d	130×120	5400×42	14.5
d	120×115	6250×41	18.6
Mean	107	5194×39 ±200	18.3

Table 13 c. *Rabbit, young, 2 months old, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
m	150× 98	7200×45	22.0
m	138×101	7400×46	24.4
d	130×130	7500×48	21.3
m	135×105	7800×45	24.8
h		7900×41	
d	150×135	8250×47	19.1
d	125×125	8500×47	25.6
d	120×120	9150×46	29.2
Mean	126	7963×46 ±240	23.8

Table 13 d. *Rabbit, male, 6 months old, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
h	165×143	7500×53	16.8
h	190×150	8300×60	17.5
m	220×180	12500×60	18.9
d		15800×59	
Mean[1]	183	11891×59 ±800	20.6

segment 3.6 and 5 mm, thick segment 7.1 ± 0.18 and 7.5 ± 0.26 mm, distal tubule 1.7 and 2 mm. The percentages are 56, 13, 25 and 6 in the male, and 54, 16, 24 and 6 in the female. The figure for each segment is the mean of 13 to 26 data, except for the thin segment. In calculating the length of this the method described on p. 262 has been employed. For this purpose a bundle of 130 long loops has been examined in the male, in the female a bundle containing 57 long loops.

[1] Including the data of table 13 i.

Table 13 e. *Rabbit, male, 8 months old, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
m	205×180	12400×64	21.5
m		12500×59	
d		12800×62	
m		13000×62	
h		13200×61	
m	220×180	13500×60	20.5
d		13600×65	
h		13800×58	
h		14900×63	
h		15000×60	
Mean		13470×61 ±260	21.0

Table 13 f. *Rabbit, female, 10 months old, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
m	210×180	14800×54	21.1
d	195×180	15800×55	24.8
d	265×210	17500×53	16.7
d	240×210	17800×58	20.5
h	225×185	18000×57	24.6
Mean[1]	200	16767×55	23.0

Table 13 g. *Rabbit, male, 10 months old, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
m	225×190	15000×56	19.6
m	165×145	15000×62	38.9
d	225×175	15000	
h	190×150	15600×63	34.5
m	240×195	16500×60	21.2
m	203×165	17300	
h	240×185	18000×68	27.9
h	225×175	18000×75	34.3
h	210×185	18800	
Mean[1]	190	16177×64 ±400	30.0

Table 13 h. *Rabbit, old female, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
h	225×225	23800×62	29.1
h	315×225	24000×62	21.0
m	225×220	25900×56	29.3
d	250×210	26300×58	29.1
m	280×205	27600×60	28.9
m	325×270	30000×64	21.9
Mean[1]	248	25971×60 ±900	26.1

The ratio of the mean lengths of the proximal tubule and the thick segment is in the "Young, 2 months old" 1.60, in "Male, 10 months" 2.25, in "Female, 10 months" 2.23, and in an about 1-year-old rabbit of mixed breed it is 2.07.

The relative volumes of cortex, outer zone and inner zone have been estimated in "Male, 8 months". The cortex forms 75 % of the total volume, the outer zone 21 % and the inner zone 4.5 % (cf. Hollatz 1922).

The rabbit kidney has been investigated repeatedly, and there is a number of descriptions of its shape and structure. These usually agree

[1] Including the data of table 13 i.

Table 13 i. *Rabbit, young 7 days old* (1), *male 6 months* (2), *male 10 months* (3), *female 10 months* (4), *old female* (5), *tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
(1) *h*	78× 59	1500×28	450× 7	1130×15	370×19	43	13	33	11	9.1
h	90× 56	1890×34	770	1500×18	450	41	17	33	10	12.8
m	90× 70	2100×38	1500	2200×19	750×25	33	23	33	11	13.3
m	84× 73	2480×37	2550×11	2050×18	460×27	33	34	27	6	15.0
d	98× 86	2780×38	3100×10	2030×20	900×25	32	35	23	10	12.5
d	95× 95	3000×38		1880×20	550×30					10.3
dd		(4200)	(8000)	(1800)	(800)	(28)	(54	12)	(5)	
(2) *hc*	195×120	9400×54	0	3700×22	850×45	67	0	27	6	21.7
d	225×170	11600×58		4500×35	975×44					17.6
m	215×190	11700×57		4600×32	1200					16.3
d	230×160	12400×60		3600×34	1300×42					20.2
m	220×150	13500×62		4350×32	1200×45					25.4
h	180×165	13800×62	2100×14	6750×37	1280×41	58	9	28	5	28.8
h	205×195	14300×63	1900	6380×37	1650×43	59	8	26	7	22.5
dd		(12500)	(21000)	(3600)	(1300)	(33)	(55)	9)	(3	
(3) *h*	190×150	14800×64	2200×10	7300×28	1900×40	56	8	28	7	33.2
h	195×160	15200×62	2500×10	8400×30	1800×38	54	9	30	6	30.2
h	175×165	15300×63	3000×11	7900×30	2000×41	54	11	28	7	33.4
d	230×190	15800×65		4800×26	1800×36					23.5
dd		(16000)	(21000)	(4500)	(2000)	(37)	(48)	(10)	(5)	
(4) *m*	205×175	15400×54		6000×29	1500×40					23.1
h	190×165	16500×53	1950	7500	2200	59	7	27	8	22.8
h	225×180	16500×56	2200×15	8000×26	2600×38	56	8	27	9	27.9
h	225×180	18600×55	1900×10	8700×28	2600×40	58	6	27	8	25.3
dd		(17800)	(20000)	(4200)	(2600)	(40)	(45)	(9)	(6)	
(5) *h*	260×240	24200×60	2700×18	12000×32	3000	58	6	29	7	23.3
dd		(27000)	(23000)	(6000)	(2500)	(46)	(39)	(10)	(4)	

with my findings. The dimensions of the kidney and the thickness of the cortex, however, are often stated to be lower than is normal in my material (Krause 1921, Jaffé 1931, Marschner 1937). This may be due to racial differences, but more probably these writers have examined young rabbits only. From the data given above it is evident that Marschner's statement (op. cit. p. 365) that rabbit kidneys may be distinguished from other kidneys by their thin cortex, is not correct.

The microscopical structure has been investigated by PETER (1909) and HUBER (1911) in particular. My findings agree qualitatively with their descriptions, but the measurements given by them, especially by PETER, are much smaller than mine made on mature specimens. PETER, however, used the kidneys of a young rabbit, only 2 months old (op. cit. p. 70). It also seems clear that his material had shrunk considerably, as is normal after maceration with the relatively weak acid he used. There can be no doubt that the figures for the length and thickness of the proximal tubule, given by PETER, are very much lower than those normally existing in a mature rabbit. This, of course, had little weight with PETER, who was more interested in the structure than in the dimensions of the tubules. It is, however, much to be regretted that these figures have been generally accepted as representative of the rabbit kidney (PÜTTER 1926, MARSHALL 1934, CONWAY 1937). The measurements given by HUBER are in closer agreement with mine, though somewhat low. The ratio of the lengths of the proximal tubule and the whole nephron is also too small, as calculated from PETER's figures.

KOLLMANN (1864) and PYE (1875) give some details of the microscopical structure, and in a paper on pathological changes in the rabbit kidney, STRONG (1940) depicts a complete, isolated, normal nephron.

Sciurus vulgaris L.

Material. The kidneys of an old male.

Form. The weight of the kidneys is 1.70 gm and the dimensions 16.5 × 11 × 8.5 mm. Papilla relatively long and pointed (fig. 7 *C*, p. 295), pelvis with processes. The cortico-medullary boundary is distinct and even. Cortex 1.8 mm, outer zone 2.6 mm and inner zone 3.8 mm thick. The outer stripe is marked and thick.

Tubules. The epithelium of the capsule is high and opaque at the transition into the proximal tubule. There is no neck, and the proximal tubule is tortuously convoluted. The distal third of the proximal tubule is differentiated into two segments. The first of these is less transparent than the preceding two-thirds of the proximal tubule, the second part, on the other hand, is lighter and more transparent than these. This last segment is often somewhat slenderer than the proximal tubule on an average.

The short loops are about as numerous as the long (24: 18). The short loops always turn in the thick segment. The difference between the thicker and the thinner part of the thick segment is small in the high nephrons also. The collecting tubules often join already in the inner part of the cortex.

Utsugi (1931 a) has investigated the tubules of the squirrel kidney. The paper is written in Japanese, and the abstract is short and in some respects obscure; a comparison is thus impossible.

Table 14. *Sciurus vulgaris, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
h	125×120	6000×52	20.8	*h*	140×155	7000×56	18.1
h		6400×49		*h*	135×150	7100×53	18.6
	150×113	6800×48	19.3	*h*	135×135	7200×55	21.7
m	150×120	6900×50	19.2		160×120	7500×50	19.5

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
	135×116	6250	1100	3500	1050	53	9	29	9	
h	150×120	6500×50	1000×6	3200×20	900×35	56	9	28	8	18.1
h	150×120	6900×42	1150×8	3900×26	1150×39	53	9	30	9	16.1
	150×130	6900×46		3300×27	1000×34					16.3
h	135×113	7100×53	1300×8	3700×24	1200×35	53	10	28	9	16.3
m	155×113	7200×52								21.4
d	158×135	7800×54		3100	1050					19.7
dd		(8000)	(9500)	(2500)	(1200)	(38)	(45)	(12)	(6)	
Mean	135	6903×51 ±120	7	3450×24	1058×36					18.9

Castor fiber L.

Material. The kidneys of four specimens in alcohol.

Form. One of the kidneys has the dimensions 60 × 36 × 21 mm. There are two papillae, only slightly projecting into the pelvis (fig. 7 *D*). The collecting ducts are very large distally, and form almost all of the apices of the papillae. The cortex is about 7 mm thick, the medulla is 14 mm. The former contains thick medullary rays, and the latter is not divided into zones. The kidneys of two of the other specimens agree in essentials with this description, but the third has only one papilla.

The tubules. The above-described kidney has been macerated. There are cortical nephrons, and the kidney seems to be devoid of long loops. There is always a pars recta, though it may be tortuous, like the main part of the proximal tubule. The transition into the thin segment occurs

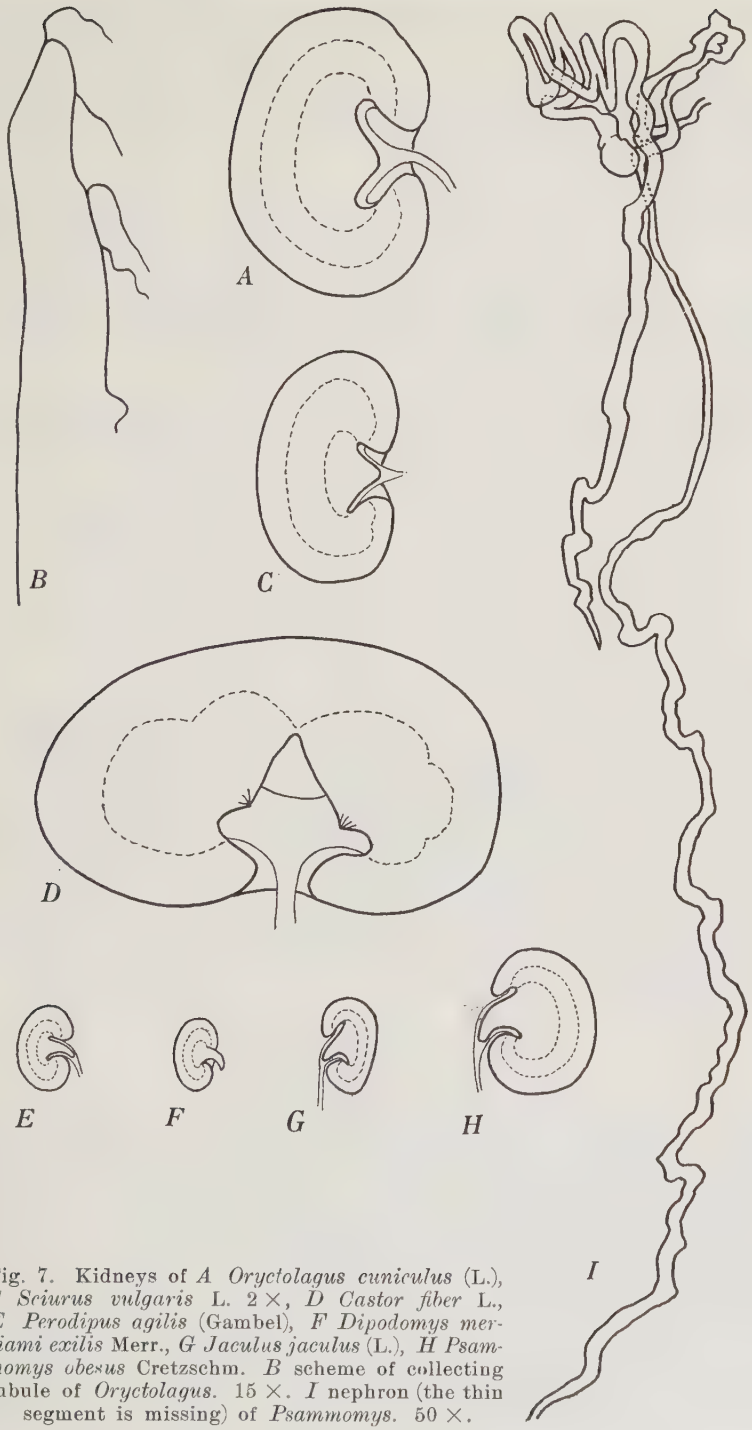


Fig. 7. Kidneys of *A Oryctolagus cuniculus* (L.), *C Sciurus vulgaris* L. 2 ×, *D Castor fiber* L., *E Perodipus agilis* (Gambel), *F Dipodomys merriami exilis* Merr., *G Jaculus jaculus* (L.), *H Psammomys obesus* Cretzschm. *B* scheme of collecting tubule of *Oryctolagus*. 15 ×. *I* nephron (the thin segment is missing) of *Psammomys*. 50 ×.

at different levels, from the middle parts of the cortex to the stripe boundary, about 2 mm below the cortico-medullary boundary. The cortical nephrons mostly have no thin segment. The loops always turn in the thick segment, which is differentiated into a thicker and a thinner part in those nephrons whose loops enter the medulla. The collecting tubules have well-developed arcades.

Some measurements of capsules and proximal tubules are given below. The distal tubules are usually 1.5—2.0 mm long and 0.035 mm thick.

The lengths of the segments of one of the deepest nephrons may be estimated at: Proximal tubule 13 mm, 41 %, thin segment 7 mm, 22 %, thick segment 10 mm, 31 %, distal tubule 2 mm, 6 %.

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
hc	94× 83	5600×41	29.4	*h*	173×120	10100×48	23.4
hc	120× 98	5800×42	20.7	*d*	175×115	11000×51	27.9
m	160×135	9800×52	23.6	*d*	165×135	13100×49	28.8
				Mean	131	9200×47	25.6

Gerhardt (1914) states that *Castor* has several tubi maximi, but no pelvis. He has, however, not been able to examine his material thoroughly, as the kidney belonged to the exhibition material of a museum. Probably as a result of this the description is somewhat obscure, and in the drawing (op. cit. Pl. I, fig. 19) nothing resembling tubi maximi is to be seen. The spaces visible there are certainly blood-vessels. It seems most probable that the section has not cut into the pelvis at all, but is lateral to it. There is no need to believe that the beaver kidney might show tubi maximi in addition to the two forms described above.

Perodipus agilis (Gambel).

Material. One pair of kidneys in alcohol.

Form. Dimensions: 11 × 7 × 5.5 mm. The pelvis is relatively large with distinct processes. The papilla is long and pointed and projects slightly into the ureter (fig. 7 *E*, p. 295). After maceration the cortex is 1.7 mm thick, the outer zone 1.9 mm and the inner zone 4.8 mm. The maceration caused a swelling of about 13 %.

The tubules. The capsule is almost round in the high nephrons, but oval in the deep ones. The proximal tubule is tortuous and passes into the thin segment at different levels in the outer stripe. There are long and short loops. The latter turn at different levels in the inner half of

the outer zone, and they turn within the thick segment. The latter always consists of a thicker and thinner part. There are often short arcades. The collecting tubules are relatively thin.

In addition to the tubules tabulated 13 more thick segments have been measured. The mean length of the thick segment is 2.9 ± 0.04 mm. A further 10 distal tubules have also been measured, and the mean length of this segment is about 0.8 mm.

Table 15. *Perodipus agilis, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
h	80×75	3100×36	18.6	*h*	100× 85	3700×34	14.8
h	90×80	3200×34	15.1	*m*	100× 90	4300×36	17.2
m	85×80	3400×36	18.0	*m*	105× 90	4400×38	17.7
h	100×70	3600×37	19.0	*d*	140×110	5700×38	14.1
m	105×75	3600×34	15.5	*d*	135×135	6700×38	14.0

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	83× 75	3200×34	1250×10	2850×24	800×25	40	15	35	10	17.5
h	85× 75	3350×36	1400× 8	2950×25	650×28	40	17	35	8	18.9
h	100× 75	3400×37	1350×12	2800×24	900×29	40	16	33	11	16.8
m	105× 75	3500×35	1400×10	3000×23	900×28	40	16	34	10	15.6
d	120× 95	4500×38		3200×27	900×30					15.0
d	130×115	5200×40		3000×25	750×30					13.9
Mean	96	4053×36 ±250	10	25	28					16.4

Dipodomys merriami exilis Merr.

Material. One pair of kidneys in alcohol.

Form. The kidneys agree in essentials with those of *Perodipus* (fig. 7 *F*, p. 295). The dimensions are 9 × 5 × 4.5 mm, and the joint depth of cortex and medulla 6 mm. After maceration the cortex is 0.75 mm thick, the outer zone 0.9 mm and the inner zone 2.9 mm.

The tubules. I have not been able to find any differences as compared with the tubules of *Perodipus*.

The dimensions of some nephrons are given in table 16. The shrinkage was about 25 % of the alcohol material. 54 short and 20 long loops

have been counted. Including 14 more proximal tubules the mean length of the proximal tubule is 1.8 ± 0.1 mm. The mean length of the thin segment of 18 long loops is 2.5 mm. The mean length of the thin segment of the short loops is 0.7 mm. The mean length of this segment, with both short and long loops included, would thus be about 1.2 mm. The mean length of the thick segment (18 measurements) is 1.4 ± 0.02 mm, and the mean length of the distal tubule about 0.35 mm. The proximal tubule constitutes about 38 % of the total tubule length in the kidney, the thin segment 25 %, the thick segment 29 %, the distal tubule 7 %.

Table 16. *Dipodomys merriami exilis, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	45×40	1500×15	700× 5	1300×12	300×15	39	18	34	8	12.5
h	45×45	1600	700	1350	350	40	18	34	8	(12.6)
h		1900×17	1800×10	1450	400	34	32	26	7	
m	55×50	2100	2500	1400	375	33	39	22	6	(15.3)
d	68×45	2250×20		1350	300					14.7
m	75×45	2400×19	2800× 8	1500×16	400×14	34	39	21	6	13.5
d	70×45	2500×21	3300× 6	1500×14	350×15	33	43	20	5	16.7
d	75×60	3600×19	5400× 8	1350×13	370×15	34	50	13	4	15.2
d	90×65	4100×20								14.0
dd	100×50	4300×19	(6500)	(1350)	(500)	(34)	(51)	(11)	(4)	16.3
Mean	59	19	7	14	15					14.7

Jaculus jaculus (L.).

Material. The kidneys of an old female, captured at Omdurman, in alcohol.

Form. The kidneys are of the common bean-shape. The papilla is long and projects into the ureter (fig. 7 *G*, p. 295). The cortex is 1.4 mm thick, the outer zone 2.1 mm, the inner zone 5.3 mm. Dimensions $12 \times 7 \times 6$ mm.

The tubules. The capsule is often oval, especially in the deep nephrons. The pars recta is always well developed and the pars convoluta is always distinct also, though it is unusually short in the high nephrons. The loops of the high nephrons turn as much as 1 mm above the zone boundary. There is very little difference between the thicker and the thinner part of the thick segment, with regard to both thickness and

structure. The thick segments are mostly wavily tortuous. The short loops often turn in the thick segment. Since the transition into the thick segment occurs at varying levels in the long loops it is often very difficult to decide if a loop is long or short. About a third of about 150 loops were certainly short, and as many long, but the remaining 50 loops could not be classified with certainty. The distal tubule and the initial collecting tubule show nothing unusual. The collecting tubules are thin and often have arcades.

Some nephrons have been measured and their dimensions are given in table 17. The longest of these nephrons nearly approaches the maximum length in this kidney, and there is certainly not more than one such nephron in hundreds. It must therefore be excluded in calculating the means. Proximal tubules with the lengths 3.6, 3.9, 4.0, 4.1, 4.2, 4.4, 5.3 mm have been measured in addition. The mean length of the proximal tubule is 4.5 ± 0.23 mm. Seven more thick segments have lengths varying from 3.5 to 4.3 mm. The mean length of this segment is (the longest nephron still excluded) 3.9 ± 0.04 mm.

Table 17. *Jaculus jaculus, tubule dimensions in* μ.

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
m	85× 70	3300×30		3200×22	750×28					16.6
h	75× 75	3600×32	1800×9	3700×23	650×27	37	18	38	7	20.5
h	95× 65	4000×35		3700×25	1000×30					22.7
d	150×105	5500×36		3600	950					12.6
dd	165×135	11000×42	(13000)	2700×23	1000×32	(40)	(46)	(10)	(4)	20.7
Mean	102	35		23	29					18.6

Microtus agrestis (L.).

Material. The kidneys of two mature specimens, a female and a male.

Form. In the female the dimensions are $12 \times 7.5 \times 5$ mm, and the weight of the kidneys is 0.48 gm. The cortex is 2 mm thick, the outer zone 2.3 mm, and the inner zone 2.3 mm. The outer stripe occupies 1.1 mm of the outer zone.

In the male the corresponding values are: $15 \times 8 \times 6$ mm, cortex 2.1, outer zone 2.8, of which the outer stripe occupies 1.4 mm, inner zone 2.4 mm. The shape of the papilla is shown in fig. 8 *A*. The pelvis has processes.

The tubules. The nephrons have long or short loops, or they are confined to the cortex. In the male the latter had loops which reached the cortico-medullary boundary, and even penetrated slightly into the outer zone. There is often a distinct neck, especially in the deepest nephrons. The thin segment is usually absent in the cortical nephrons, and is very short in the high short loops (cf. fig. 8 *B*). The transition into it occurs at varying levels, from the cortico-medullary boundary to the

Fig. 8. *A* Kidney of *Microtus agrestis* L. *B* High nephron of *Evotomys glareolus* Schreb. 50 ×.

stripe boundary. The transition into the thick segment occurs in the high short loops already in the outer stripe. In the female the thick segments of the cortical nephrons are not differentiated into a thicker and a thinner part, but in the male all nephrons show a differentiation of this kind. The short loops always turn within the thick segment. The collecting tubules sometimes have arcades, and normally 4 or 5 nephrons join each collecting tubule. The first central junctions may occur in the central parts of the cortex, but usually they are found in the outer zone.

In the male there is a swelling of about 10 % after maceration. In the female there are 16 cortical nephrons out of 160 nephrons examined, and 23 have long loops. In the male 120 nephrons have been

Table 18 a. *Microtus agrestis, female, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
h	138×115	3900×31	7.6	*m*	162×130	4600×31	6.8
m	140×110	4000×35	9.1	*m*	158×120	4700×35	8.7
h	120×120	4000×34	9.4	*d*	145×135	4900×38	9.5
m	143×135	4100×36	7.6	*m*	150×135	4900×32	7.7
m	158×135	4600×37	8.0	*d*	145×140	6000×36	10.6

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
hc	113× 98	2200	0	1000×26	500	59	0	27	14	
hc	113×105	2300×30	0	1100×26	500×38	59	0	28	13	5.8
h	135×110	2900×30	75× 7	1600×22	600×38	56	1.5	31	12	5.9
hc	129×110	2950×29	0	1400×26	700×34	58	0	28	14	6.0
h	120×100	3000×31	75×10	1700×24	600	56	1.4	32	12	7.8
h	143×110	3200×30	80× 8	1800×22	600×40	56	1.4	32	11	6.1
h	120×120	3300×31	50× 6	1650×23	640×38	59	1.0	29	11	7.1
m	130×115	3600×32	300	2000×23	700×38	55	5	30	11	7.7
h	120×120	3700×31	40×20	1600×26						8.0
m	135×120	3900×32			825×31					7.7
d	165×130	4700×38		2225×26	800×32					8.3
d	150×150	5600×36		2200×30	800×40					9.0
dd	165×165	6600×37	(5400)	2400×26	(900)	(43)	(35)	(15)	(6)	9.0
Mean	131	4072×33 ±230	10	1723×25	660×37					7.9

examined in this respect. 15 are cortical nephrons; 95 loops are short, and 10 long. The mean lengths of the segments are difficult to estimate, since the variations are very great. In the female the mean length of the proximal tubule is about 4.1 mm. The thin segment is 0—1 mm long in the high nephrons, and the average value is probably about 0.4 mm. In the long loops the length varies from 1.3 to 5 mm, and since the longest loops are very few, the average is probably not over 2 mm. The average length of the thin segments of all nephrons is then about 0.6 mm. Correspondingly, the length of the thick segment is estimated at 1.8 mm, and the length of the distal tubule at about 0.7 mm. The proximal tubule should thus occupy 56 % of the total tu-

Table 18 b. *Microtus agrestis, male, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
hc	100×100	3700×51	0	1900×27	650×40	59	0	30	10	18.9
h	115×100	3800×52	230×20	2500×26	600×40	53	3	35	8	17.1
h		4050×50	350×15	2600×24	675×44	53	5	34	9	
d	110× 95	4200×53	1100×15	3200×29	800×42	45	12	34	9	21.3
m	115×100	4600×49	780×13	3000×31	850×37	50	8	33	9	19.6
d	130×100	4800×55		3200×28	900×41					20.3
m	110× 90	4900×52	540×12	3300×30	750×43	52	6	35	8	25.7
d	135×115	5200×55	1300×10	3250×34	750×45	50	12	31	7	18.4
d	120×100	5400		3000×30	800×38					
Mean	108	4517×52	14	2883×29	753×41					20.2

bule length, the thin segment 8 %, the thick segment 25 % and the distal tubule 10 %. Though the uncertainty of these figures is great, they may have some value for comparison purposes. In the male the thick segment is plainly somewhat longer than in the female.

Table 19. *Evotomys glareolus, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
hc		2800×38	0	1100×16	700×24	61	0	24	15	
hc	96×88	3100×41								15.0
hc	96×60	3100×38	0							20.5
h	88×72	3100×40	20× 8	1100×20	650×25	64	0.4	23	13	19.6
h	88×65	3100×41	250× 7	1600×16	700×23	55	4	28	12	22.2
h	90×75	3300×40	20×10	1400×20	720×24	61	0.4	26	13	19.6
hc	96×72	3400×39	0	1100×15	700×26	65	0	21	13	19.2
m	96×70	3400×40								20.2
d	120×80	3600×41								15.4
d	96×80	4000×40								20.8
Mean	85	3290×40 ±110	8	1260×17	694×24					19.2

Evotomys glareolus Schreb.

Material. The kidneys of a mature female have been macerated.

Form. The kidneys agree in shape with those of *Microtus*. Weight 0.32 gm.

The tubules. The tubules agree in essentials with those of *Microtus* (fig. 8 *B*, p. 300). The thick segment of the cortical nephrons is not differentiated into thicker and thinner parts, and their loops reach the cortico-medullary boundary.

Arvicola terrestris (L.).

The kidneys of this species also agree qualitatively with those of *Microtus agrestis*, as regards both shape and microscopical structure.

Epimys rattus (L.).

Material. The kidneys of an old female of the common white rat.

Form. Dimensions 19.5 × 13 × 10 mm. Weight 2.9 gm. The papilla is pointed (fig. 9 *A*, p. 307) and the pelvis has processes. The cortex is distinctly and evenly demarcated, 2.9 mm thick, the outer zone 2.6 mm, the inner zone 5.4 mm.

The tubules. The capsule is round or oval. There is no neck. The proximal tubule is very tortuous, with many bends (Pl. 1, fig. 5). The

Table 20. *Epimys rattus, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
d	195×145	9000×51		4900×28	900×43					16.2
m	180×135	9000×52		5100×26	1300×41					19.3
m	180×135	9500×50		5000×29	1600×38					19.5
h	180×165	9800×48		5700						15.8
h	180×140	9800×49		5800×26	1400×39					19.1
h	185×125	10100×53		6000×25	1600×38					23.1
h	180×160	10200×47	1700×15	6000×26	1500×39	53	9	31	8	16.6
h	180×135	10300×50	2000×14	5300×26	1400×40	54	11	28	7	21.2
m	155×150	10600×49		5200×25	1350×44					22.3
dd	205×165	12000×54	(12000)	4900×29	1600×40	(39)	(39)	(16)	(5)	19.2
Mean	164	10030×50 ±270	15	5390×27 ±140	1406×40					19.2

terminal part of the proximal tubule is, normally, distinctly thicker than the rest of this segment, but tapering towards the transition into the thin segment. The proximal tubule has often small protuberances. The thick segment is as a rule relatively tortuous in its thicker part. The latter is indistinctly differentiated from the thinner part. The distal tubule is strongly and irregularly looped, and its surface often shows small projections. The initial collecting tubule is often absent. The collecting tubules are most often formed by the junction of 6 nephrons and, normally, have a small arcade, and some direct junctions. The long loops constitute 28 ± 4.5 % of the total number.

The kidneys of the white rat have been examined with maceration methods by Utsugi (1931 b), and by Walker and Oliver (1941). I have had access to Utsugi's paper in abstract only. The abstract is very short and does not permit any discussion of the inconsistencies between Utsugi's description and mine.

Walker and Oliver have isolated a number of the highest nephrons of rat kidneys (and guinea-pig kidneys). They give the dimensions of some nephrons. These agree relatively well with my measurements, but on the whole the thin segment is shorter and the distal tubule is longer in their material.

Mus musculus L.

Material. The kidneys of several specimens have been examined, some of them after maceration.

Form. The kidneys differ from those of *Mus flavicollis* and *sylvaticus* only in the shape of the papilla, which is distinctly longer and more pointed in this species (fig. 9 *B*, p. 307). It normally projects into the beginning of the ureter. The kidney weight ranges from 0.20 to 0.35 gm in mature specimens. In the most minutely examined specimen it is 0.23 gm, and the dimensions 9 × 5.5 × 4.5 mm. The cortex is 1.3 mm thick, the outer zone 1.2 mm and the inner zone 3.7 mm.

The tubules. The tubules agree closely with those of *M. flavicollis* and *sylvaticus* (cf. p. 306). On the whole the tubules seem to be more looped than the tubules of these forms, also when specimens of corresponding ages are compared.

The percentage of long loops is 24 ± 3.6.

The mean length of the proximal tubule is probably slightly lower than the mean of table 21, since the deep nephrons are too numerous in the table. The true mean may be estimated at about 4.0 mm. The thick segment has been measured in 10 nephrons. The mean is 2.0 ± 0.05 mm. The distal tubule is, on an average, 0.6 mm long. The ratio of proximal tubule and thick segment is 2.00, if the corrected

Table 21. *Mus musculus, tubule dimensions in μ.*

Capsule	Prox. tubule	Ind.	Capsule	Prox. tubule	Ind.	Capsule	Prox. tubule	Ind.
112× 80	3400	(15.6)		3760×40		112× 96	4300×42	16.8
112× 88	3440×40	14.0	105× 95	3800×43	18.1	110× 88	4320	(18.3)
104× 90	3500	(15.3)	112× 90	3840×40	15.2	120× 80	4320×42	18.9
96× 88	3520×40	16.7	105× 95	3900×41	17.7	120×100	4950×42	17.3
120× 85	3550	(14.3)	112× 96	3920×41	14.9	120×112	5200×42	16.3
104× 88	3600	(16.1)	104× 88	4000	(17.9)	120×105	5340×44	18.6
112× 80	3680	(16.8)	112×104	4000×42	14.4	125× 90	6000	(21.9)
104×104	3680×40	13.6		4000×41		136×104	6880×44	21.4
120× 96	3700×42	13.5	105×100	4160×42	16.6	130×130	8550×42	21.2
120× 88	3760	(14.6)	120× 90	4180×41	15.9			

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	90×75	3600×37	450×5	1900×21	500×35	56	7	29	8	19.7
h	90×75	3700×33	500	1950×19	500×30	56	8	29	8	18.1
dd		(8550)	(8000)	(1500)	(1000)	(45)	(42)	(8)	(5)	
Mean	103	4276×41 ±200								16.9

figure for the proximal tubule is accepted, or 2.15 ± 0.10 if no correction is applied.

The kidney of *Mus musculus* has been repeatedly examined by various authors. The form of the papilla is shown in a figure by Hamburger (1890). The microscopical structure has been investigated in particular by Peter (1909). The agreement with my findings is close, quantitatively also. The variation in length of the proximal tubules, however, does not appear from his data. v. Möllendorff (1922) emphasizes this feature, which is clearly shown by his material, and also by Peters' data (1928). The latter author gives relatively very low values for the dimensions of the capsule. This raises the ratio of the surfaces of the proximal tubule and the capsule of a single nephron up to 70, with means of this ratio up to 49. It is difficult to explain this fact. It may have some connection with her taking the kidneys from the living animal, since it is possible that the glomeruli contract more than normally in this procedure. It is possible also that her technique, which includes mounting in glycerine-

jelly, has a part in this. Almost certainly it is one cause of the great variation shown by her data.

Schweigger-Seidel (1865) and Rindowsky (1867) have also examined mouse kidneys. The paper by Auerbach (1925) contains little that had not already been mentioned by Peter (1909).

Mus flavicollis Melch.

Material. The kidneys of a number of young and old specimens.

Form. The total kidney weight varies from 0.32 to 0.78 gm in mature specimens of my material. The lowest weights occur in young specimens, and the highest in old. The dimensions are normally about 11 × 6.5 × 4.5 mm. The cortex is 1.4—2.0 mm thick, the outer zone 1.0—1.4 mm, the inner zone about 3—4 mm. It may be mentioned that the central part of the cortex does not contain any glomeruli, as is often the case in other species also. The following specimens have been more thoroughly examined after maceration.

	Dimensions, mm	Cortex, mm	Outer zone, mm	Inner zone, mm	Weight, gm
Young male	9.5×5.5×4	1.2	1.1	3.3	0.23
Female	11 ×6.5×4.5	1.4	1.3	3.1	0.40
Male	12 ×7 ×5	1.5	1.3	3.0	0.42
Old male	12 ×8 ×5.5	1.8	1.2	3.2	0.54
Old female	14 ×8 ×6	1.9	1.7	2.8	0.74

The pelvis is provided with distinct processes and the papilla is pointed. In young specimens the papilla is longer and more slender than in old ones (fig. 9 *C*, *D*, *E*).

The tubules. There is no neck. The proximal tubule is on the whole of uniform thickness, but the last part of it may be thicker or slenderer than the preceding parts. This terminal segment has normally a more transparent epithelium, but the difference is small, and the transition gradual. The transition into the thin segment is abrupt and, normally, occurs at the same level in all nephrons. The short loops turn slightly peripheral to the zone boundary and the bend lies at or near the transition between thin and thick segment (Pl. 2, fig. 2, 3). The thick segment of the high nephrons is differentiated into a thicker and a thinner part, but in the "Young male" this differentiation is faint. In this specimen there is normally also an intercalated segment which is absent in

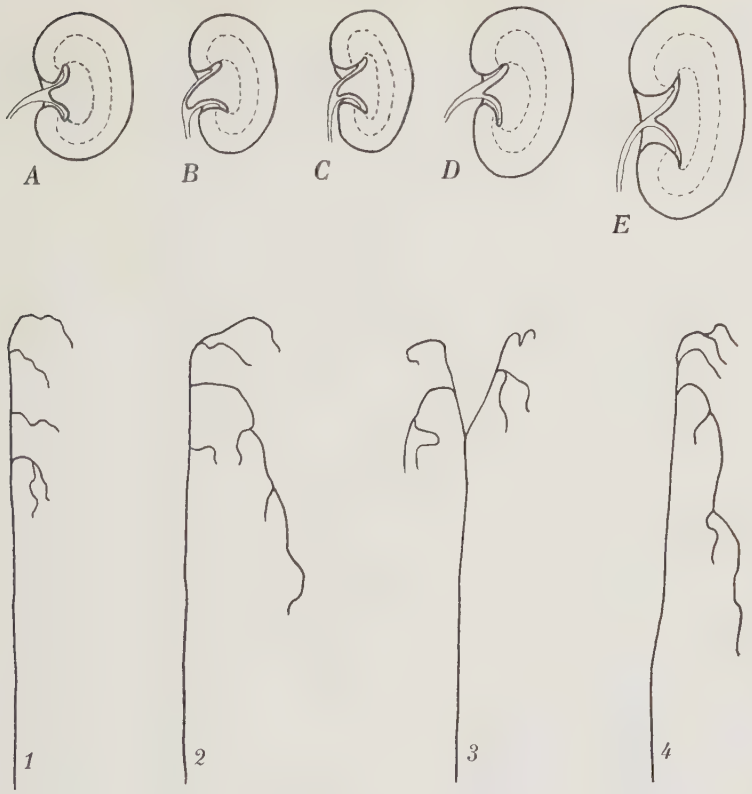


Fig. 9. Kidneys of *A Epimys rattus* (L.), *B Mus musculus* L. 2 ×, *C, D, E Mus flavicollis* Melch. 2 ×. Collecting tubules of *Mus sylvaticus* L. *1, 2, 3, 4* about 40 ×.

the others. The collecting tubules are often formed by direct junctions, but small arcades are also common (cf. fig. 9: *1, 2, 3, 4*). The collecting tubules are relatively thin, 0.020—0.030 mm, except in the inner parts of the medulla, where they are thicker.

The percentage of long loops is: "Young male": 20.2 ± 3.1 %, "Female": 19 ± 2.8 %, "Male": 27 ± 4.3 %, "Old male": 23 ± 2.9 %, "Old female": 18.3 ± 3.0 %.

In the "Young male" there was a swelling to about 10 %.

Thus the mean length of the proximal tubule is 3.2 mm. The uncorrected mean is 3.53 ± 0.030 mm. The mean length of the thin segment has been calculated from measurements of 16 short and 4 long loops. It is 0.89 mm. The thick segment, also calculated from 20 measurements, is 1.84 ± 0.035 mm long, and the distal tubule 0.57 mm. The proximal tubule forms 52 %, the thin segment 13 %, the thick segment 27 %, and the distal tubule 8 % of the total length of the tubules. The value for the thin segment is the least reliable of these figures. In the

Table 22 a. *Mus flavicollis, young male, proximal tubule lengths in small samples.*

Sample	High (h) and middle (m) proximal tubules, length in mm																						Deep prox. tub. length in mm	Mean length
	2.8		2.9		3.0		3.1		3.2		3.3		3.4		3.5		3.6		3.7		3.8		3.9		4.0			
	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m	h	m		
a					1					2	1		1	1			1										3.7 4.8	3.511±0.176
b							1		3		2		1					1		1							3.9 4.4	3.482±0.115
c					1								3	1	1	1											4.4	3.500±0.140
d						1	1			1	1				1	1			1								3.8 3.9	3.444±0.105
e	1		1		1			1				1						1		2	1						3.9 4.5 5.0	3.608±0.189
f								1	1		1		1	1	1	1											4.4	3.475±0.141
g					1		1			2	1					1											4.4	3.385±0.179
h			1		1		1			1		2	1				1										4.5 5.3	3.560±0.240
i			1		1				1	1	1	1	1														3.9 4.1	3.368±0.132
k					1				1					1	1			1		1	1		1				4.3 5.2	3.760±0.197
l			1						1				1	1			2	1									3.7 4.4	3.533±0.136
m					3					1	1									1							3.6 4.3	3.388±0.162
n							1		2		1										1	1					3.9 4.6	3.613±0.181
o					1		1			1	1		1		1	1		1							1		4.9 5.0	3.682±0.208
p							1		1		1	2		1	1		1										4.7 5.3	3.670±0.231
	1		4		12		9		19		17		16		11		10		6		4		1		1			3.532±0.030

Table 22 b. *Mus flavicollis, young male, distribution of deep prox. tubules according to length, including those of table 22 a.*

Length in mm	3.6	3.7	3.8	3.9	4.0	4.1	4.2	4.3	4.4	4.5	4.6	4.7	4.8	4.9	5.0	5.1	5.2	5.3	5.4	5.5	5.6	5.7	5.8	5.9
Number of tubules	3	6	6	10	2	7	2	4	7	5	4	2	3	3	2	0	2	3	0	0	1	0	1	1

Table 22 c. *Mus flavicollis, young male, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
h	77×62	2800		*h*	96× 73	3500	
h	80×76	2900		*m*	105× 75	3500	
h	87×75	3000×33	15.2	*h*	84× 73	3500	
h	75×68	3000×35	20.6	*m*	98× 82	3500	
h	85×80	3000		*m*	95× 90	3500	
h	80×70	3000		*h*	80× 65	3600×34	23.5
m	83×82	3000		*m*	90× 90	3600×35	15.6
h	84×76	3100×34	16.5	*m*	94× 76	3600	
h	84×83	3100		*m*	90× 82	3700×36	18.0
m	90×75	3100		*h*	90× 68	3700	
m	85×82	3100		*m*	105× 75	3700	
h	82×74	3100		*m*	95× 90	3700	
m	93×77	3200×35	15.6	*d*	113× 83	3700×35	13.8
m	90×75	3200×34	16.1	*d*	105× 91	3700×34	13.2
h	85×68	3200×35	19.4	*h*	87× 82	3800	
h	83×83	3200×36	16.7	*d*	120× 90	3800	
h	90×69	3200×35	18.0	*d*	115× 94	3900×35	12.6
m	97×73	3200		*d*	108× 85	3900	
h	89×76	3200		*d*	109× 83	3900	
m	84×82	3200		*d*	102× 88	3900×37	16.1
h	86×75	3300×35	17.9	*d*	113× 90	4400×36	15.6
h	84×77	3300×35	17.9	*d*	114×105	4400×36	13.2
h	85×73	3300×35	18.6	*d*	120× 84	4400	
h	89×74	3300		*d*	115×105	4400	
m	79×76	3300		*d*	105× 90	4400×36	16.8
h	75×75	3300		*d*	115× 84	4500	
h	89×80	3300		*d*	115×100	4500	
h	90×75	3400×35	17.6	*d*	115× 94	4500×37	15.4
m	90×84	3400×37	16.6	*d*	135×120	4700×40	11.6
h	76×76	3400×36	21.2	*d*	118× 87	4800×36	16.8
m	97×72	3400×33	14.6	*d*		4800×38	
h	92×76	3400×35	17.0	*d*	125×100	4900×38	15.4
h	90×81	3400×34	15.9	*d*	122×114	5000	
h	88×74	3400×36	18.8	*d*	130×115	5200×41	14.3
m	85×72	3400		*d*	120×115	5300	
h	90×76	3400		*dd*	150×120	5800×46	14.8
m	95×81	3500×36	16.4	*dd*	135×125	5900×45	15.7
h	82×75	3500×34	19.3	Mean		36.1	16.55

Table 22 d. *Mus flavicollis, male, tubule dimensions in μ.*

Capsule	Prox. tubule	Ind.	Capsule	Prox. tubule	Ind.	Capsule	Prox. tubule	Ind.
83×68	1730×36	11.0	105×83	3530×38	15.4	160× 90	5250×40	14.6
118×75	3150×38	13.5	100×83	3680×37	16.4	120×120	5330×40	14.8
98×80	3200×38	15.5	120×91	3750×39	13.4	154×103	5360×41	13.9
118×83	3230×36	11.9	101×90	3850×39	16.5	148× 98	5550×41	15.7
90×94	3380×37	14.8	105×87	4130×38	17.3	158×112	6300×45	16.0
105×93	3450×38	13.4	122×90	4150×39	14.7	150×131	6380×44	14.3
93×94	3500×38	15.2	131×98	4500×40	14.0	158×120	6450×44	15.0

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h		3080×38	420×10	2250×22	600×25	49	7	35	9	
h	113×113	3300×38	410×10	2030×22	650×30	52	6	32	10	9.8
m	120×112	3600×41	1500×10	2250	675	44	19	28	8	11.0
h	113×100	4050×38	375× 9	2100×23	820×29	55	5	29	11	13.6
m	125×113	4350×40	1300×10	2200×24	700×31	51	15	26	8	12.3
m	128×105	4500×42	1500× 9	2300×22	750×28	50	17	25	8	15.0
	135×105	4700	1400	2000	550	54	16	23	6	13.3
m	150×120	4950×41	2050× 8	2180×23	900×28	49	20	22	9	11.3
d	150×128	5150×41	2900× 9	1750×22	750×30	49	27	17	7	11.0
d	150×120	5480×39	3200× 9	2400×23	900×30	46	27	20	8	11.9
dd		(6500)	(7000)	(1500)	(1000)	(41)	(44)	(9)	(6)	
Mean	112	4291×39.5 ±200	9	2146×23 ±59	730×29					13.9

"Female" 10 proximal tubules, mean 4.6 ± 0.2 mm, and 10 thick segments, mean 2.35 ± 0.06 mm, have been measured. The ratio of these means is 1.96 ± 0.10. This ratio is 1.92 ± 0.044 in the "Young male".

The low nephrons are somewhat too numerous in the measured sample of the "Male". The mean length of the proximal tubule is thus lower than the mean of table 22 d, i. e. about 4.0 mm. The thin segment of the short loops is about 0.4 mm long, and of the long loops about 2 mm; the weighted mean of these is about 0.8 mm; the thick segment is 2.1 mm and the distal tubule 0.7 mm long. If these estimations are correct the mean tubule has the following composition: Proximal tubule 53 %, thin segment 11 %, thick segment 28 %, distal tubule 9 %. In

Table 22 e. *Mus flavicollis, old male, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	110× 95	4350×44	450× 9	2800×23	800×34	52	5	33	10	18.3
m	120× 80	4350×42	800×10	2700×22	1100×31	49	9	30	12	19.0
m	105× 95	4500×45	550× 8	2700×21	800×36	53	6	32	9	20.3
h	110×100	4600×43	600× 9	2400×23	850×34	54	7	28	10	18.0
h	115× 95	4700×42	600× 8	2600×23	900×34	53	7	30	10	18.1
h	115×100	4700×42	650×10	2700×22	750×33	53	7	31	9	17.2
m	105× 95	4700×41	550× 8	2900×20	800×32	53	6	32	9	19.3
h	105×100	4900×43	500× 8	2750×24	850×31	54	6	31	9	20.1
d	115× 85	5200×46	2000× 9	2800×21	750×34	48	19	26	7	24.5
d	130×100	5300×43	3400× 8	2800×20	900×30	43	27	23	7	17.5
dd[1]	165×100	7500×50	6500× 9	1900×25	1300×35	44	38	11	8	22.7
Mean	104	4730×43 ±120	1010× 9	2715×22 ±50	850×33					19.2

Table 22 f. *Mus flavicollis, old female, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
h	135×115	5500×52	18.4	*m*	150×130	6100×56	17.5
h	140×110	5600×56	20.4	*d*	150×120	6200×58	20.0
h	130×110	5600×54	21.1	*m*	165×135	6400×55	15.8
h	135×120	5900×55	20.0	*h*	165×115	6600×56	19.5
m	130×105	6000×57	25.1	*d*	170×135	7400×59	19.0
				Mean	133	6130×56 ±180	19.7

the "Old male" the nephrons of table 22 e, except the deepest one, formed a single small piece, not containing other nephrons. There was a swelling of about 10 %. A "mean tubule", calculated from these 10 nephrons, has the following composition: Proximal tubule 51 %, thin segment 11 %, thick segment 29 %, distal tubule 9 %.

In the "Old female" the thin segment is 0.65—0.95 mm in the short loops; on an average 0.8 mm long. In the long loops the thin segment is most often about 2.5 mm or shorter. As some thin segments are very

[1] Not included in the mean.

long, the average length in long loops is perhaps nearer 3 mm than 2.5 mm. The average length when both long and short loops are included is about 1.2 mm. The mean length of the thick segment is 3.1 ± 0.07 mm (13 data), and the distal tubule is about 0.84 mm long.

The mean tubule ought to have this composition: Proximal tubule 54 %, thin segment 11 %, thick segment 28 %, distal tubule 7 %. The ratio of proximal tubule and thick segment in the last three specimens is 1.90, 1.74 ± 0.05 and 1.97 ± 0.08 respectively.

Mus sylvaticus L.

Material. Several specimens have been examined, but only one kidney has been macerated.

Table 23. *Mus sylvaticus, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
h	70×55	2600×28	18.9	*h*	96× 80	3700×32	15.4
h	80×72	2700×30	14.1	*h*	110× 80	3700×32	13.5
h	80×70	2900×32	16.6	*h*	143× 95	3700×42	11.4
m	80×65	3000×29	16.7	*m*	82× 66	3800×34	26.7
h	90×65	3000×31	15.9	*m*	90× 80	4000×32	19.4
m		3150×38		*d*	100× 90	4100×37	14.6
h	98×62	3500×35	20.2	*d*	150×120	4700×42	11.0
h	90×72	3600×32	17.8	*d*	150×135	6700×40	13.2

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	100× 65	2600×28	400× 5	1500×18	500×25	52	8	30	10	11.2
h	80× 70	3100×32	8	1800×18	600×20					17.7
h	105×100	3150×37	550× 8	1730×25	980×28	49	9	27	15	11.1
h	112×103	3680×38	600× 7	2030×24	1050×26	50	8	28	14	12.1
m	100× 90	3800×31		1400×18	450×22					13.1
h	132× 95	4100×38	600×11	2000×24	1000×30	53	8	26	13	12.4
d	133× 95	4400×40		2100×22	1100×33					13.9
d	136×110	5900×42		1800×26	1400×28					16.6
d	160×143	6900×45		2000×25						13.6
dd		(6900)	(6400)	(1800)	(1500)	(42)	(39)	(11)	(9)	
Mean	97	3859×35 ±230	8	1820×22 ±80	24					15.3

Form. The agreement with *Mus flavicollis* (fig. 9, p. 307) is very close. In a young male the kidneys weigh 0.25 gm. Dimensions 9.5 × 5.5 × 4 mm, cortex 1.2 mm thick, outer zone 1.3 mm, inner zone 2.7 mm.

The tubules. These agree in essentials with those of *M. flavicollis* (cf. fig. 9: *1—4*). The long loops constitute 17.3 ± 2.4 % of the total number.

The ratio of the mean lengths of the proximal tubule and the thick segment is 2.12 ± 0.16.

Hydromys chrysogaster E. Geoffr.

Material. Two pairs of kidneys in alcohol.

Form. Dimensions of one kidney, which has later been macerated: 25 × 15.5 × 8 mm. The cortex is 2.7 mm thick, the outer zone 2.1 mm, the inner zone 3.7 mm. The area cribrosa lies on a short crest (fig. 10 *L*, p. 317). The surface of the kidney shows a groove ventrally (fig. 10 *M*).

The tubules. The tubules resemble those of *Epimys rattus* in most respects. There is no distinct terminal part of the proximal tubule. The thick segment is markedly differentiated into a thicker and a thinner part. It has not been possible to ascertain the relative frequencies of long and short loops. The dimensions of some proximal tubules are given below:

	Capsule	Prox. tubule	Ind.
m	100× 90	6900×40	30.7
h	120× 90	7500×41	28.5
m	105× 99	7900×38	31.8
d	130×110	8400×39	22.9
Mean	104	7675×40	28.5

6 further proximal tubules have been measured, which are 7.1, 7.2, 7.2, 7.4, 7.5 and 8.0 mm long. The mean is 7.51 ± 0.15 mm. The mean length of 6 thick segments is 4.1 mm. The distal tubule is usually about 1.2 mm long.

A swelling of about 10 % occurred.

Psammomys obesus Cretzschm.

Material. The kidneys of an old female and a young male, in alcohol.

Form. The dimensions are, in the female, 19 × 14 × 9 mm and, in the male, 17 × 10 × 7 mm. The cortex is, after maceration, 2.2 mm thick

in the female, the outer zone 2.5 mm, the inner zone 12 mm. Before maceration the layers could not be clearly distinguished, but their joint depth was 16 mm in the female and 13 mm in the male. The papilla is very strongly developed, (fig. 7 *H*, p. 295), long and broad, and projects into the ureter.

The tubules. There are long loops only. The pars recta of the proximal tubule is always well developed. The transition into the thin segment occurs at different levels in the outer stripe. The loops do not turn in the outermost parts of the inner zone. The thick segment is always differentiated into a thicker part in the outer zone, often wavily tortuous, and a thinner, straight part in the cortex (fig. 7 *I*). There is often a distinct initial collecting tubule. The collecting tubules are fairly thin and have small arcades normally.

The dimensions of some nephrons are given in table 24. It has not been possible to isolate complete nephrons, since the thin segments were connected with one another and numerous blood-vessels in the medulla by tough connective tissue. Further proximal tubules with the lengths 3.2, 3.3, 3.5, 3.7, 4.0, 4.3 mm have been measured, as also thick segments with the lengths 4.1, 4.1, 4.3, 4.6, 4.7, 4.8 mm. Including these the mean length of the proximal tubule is 4.2 ± 0.4 mm and of the thick segment 4.6 ± 0.1 mm. The ratio of these means is 0.91 ± 0.09. It is not possible to give any estimation of the mean length of the thin segment. It must, however, be relatively enormous as compared with normal forms. This is shown by an estimation of the length of a nephron

Table 24. *Psammomys obesus, female, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Ind.
h	135× 85	3100×33				8.9
h	105× 90	3300×35		4600×23	700×25	12.2
h	115× 88	3400×34		5200×26	750×27	11.4
h	120×100	3400×37		5000×25	800×30	10.5
m	120×110	3600×36	15	4800×25		9.8
h	130× 90	3800×38		5100×24	830×27	12.3
m	165×112	4900×40		4100×25	1000×27	10.6
d	175×170	5100×41	20	4700×26	900×28	7.0
d	150×135	5600×40		3900×30	550×28	11.1
dd	215×165	9000×45	(26000)	(4000)	(1000)	11.4
Mean	129	38	18	26	27	10.5

reaching the apex of the papilla. The proximal tubule occupies 23 % only of the total length, the thin segment 65 %, the thick segment 10 % and the distal tubule 3 %.

Hystrix cristata L.

Material. Three pairs of kidneys in alcohol.

Form. The shape of the kidneys is different in the three specimens. In a young specimen they are oblong, 43 × 20 × 14 mm, in the other two the dimensions are 45 × 30 × 20 mm and 70 × 43 × 29 mm. The pelvis is small, without processes. In the first and last of the kidneys there are short ducts opening at the extremities of the area cribrosa (fig. 10 *O*, p. 317). In the second specimen I have not been able to find such structures, which are presumably small tubi maximi. The cortex is thick and has many large medullary rays. The medulla is not divided into an outer and an inner zone. In the largest kidney the cortex is about 8 mm thick and the medulla about 12 mm, in the second largest kidney the corresponding values are 7 mm and 12 mm, and in the smallest 4 mm and 6 mm.

The tubules. Maceration preparations have been made from all these kidneys, but as it has been possible to isolate fragments only from the largest one, and as the smallest kidney is obviously not fully developed, the following description mainly refers to the third kidney. There are cortical nephrons, and long loops have not been found in any one of the kidneys examined. The proximal tubules are tortuously looped and pass into the thin segment at very varying levels. In the highest nephrons this transition occurs in the middle parts of the cortex, and in the deepest nephrons as far as 3 mm below the cortico-medullary boundary. The terminal part of the proximal tubule is clearly differentiated from the preceding parts. It suddenly becomes somewhat thicker, and is more transparent (Pl. 2, fig. *1*). The thin segment is absent only in a few of the highest cortical nephrons, but is very short in most nephrons. The collecting tubules are thick and have well-developed arcades.

After maceration swelling to about 10 % occurred. Some proximal tubules have been isolated and measured (table 25). Thick segments have also been measured. The lengths are 7.0, 7.3, 8.0, 8.5, 9.0, 9.5, 9.8, 11.0 mm. The mean is 8.8 ± 0.5 mm. The distal tubules are 1.4—2.5 mm long. In one of the nephrons reaching the area cribrosa the proximal tubule may be assumed to be 13.4 mm long, the thin segment 8 mm, the thick segment 11 mm, and the distal tubule 2.5 mm. The percentages are then 38, 23, 32, and 7 respectively.

Table 25. *Hystrix cristata*, *tubule dimensions in* μ.

	Capsule	Prox. tubule	Ind.
h	205×175	12000×60	20.1
d	260×225	12000×68	13.9
h	200×170	12200×63	22.6
d	265×195	12500×70	16.9
m	260×220	12800×70	15.7
d	260×225	13000×70	15.6
h	205×175	13200×62	22.8
m	250×230	13400×67	15.6
Mean	220	12638×66 ±200	17.9

Rodentia, survey of the form of the kidney.

The statements in the literature on the kidney of the rodents are few, except those referring to rabbit, guinea-pig and rat. Only Hyrtl (1872) and Gerhardt (1914) have examined several forms.

The *Duplicidentata* examined, i.e. *Lepus* (Hyrtl), *Oryctolagus* and *Ochotona*, have one well-developed papilla, and the pelvis has processes. The medulla is differentiated into an outer and an inner zone. In most *Simplicidentata* the kidneys, too, show this structure. The relatively few deviating forms are treated below. *Aplodontia rufa* (Raf.) has a very small pelvis devoid of processes. In its lateral wall lies the small oblong area cribrosa (fig. 10 *A*). *Castor* has one or two papillae (cf. p. 294). In *Hydromys chrysogaster* E. Geoffr. the area lies on a short crest (fig. 10 *L*). *Hystrix cristata* has a low crest and may possess small tubi maximi (fig. 10 *O*) (cf. p. 315). In *Erethizon dorsatus* L. I have found a short crest, but Gerhardt (1914) says there is a papilla in this species. In *Atherura africana* Gray he finds a crest (op. cit.). *Hydrochoerus capybara* (Erxl.) and *Coelogenys paca* L. have long kidneys with two long tubi maximi (cf. Gerhardt 1914). In *Hydrochoerus* these tubi maximi open at the ends of a short crest (fig. 10 *R*), but in *Coelogenys* a crest can scarcely be said to exist, and the tubi open very near one another, forming a common pore in the wall of the pelvis (fig. 10 *S*). The pelvis has no processes in these forms. Like them *Dasyprocta aguti* L. has tubi maximi, though they are small (fig. 10 *P*), but *Cavia* (Gerhardt 1914), *Chinchilla* and *Dolichotis* each have one papilla (fig. 10 *U*, *T*). *Myocastor* has a crest (fig. 10 *V*, and also Gerhardt 1914). The simple kidney with a papilla

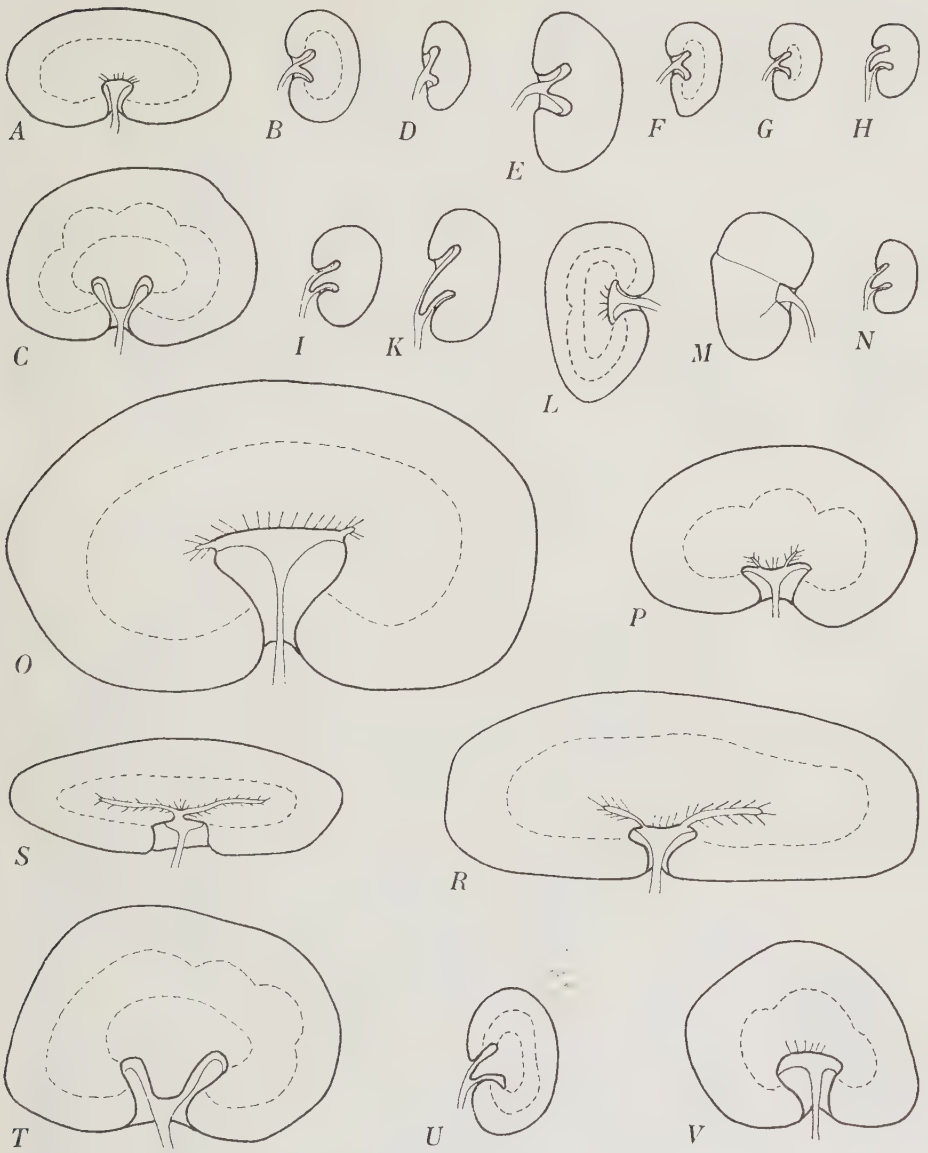


Fig. 10. Kidneys of rodents. *A Aplodontia rufa* (Raf.). *B Geomys tuza* (Ard.). *C Pedetes caffer* (Pall.). *D Spalax typhlus* Pall. *E Cricetus cricetus* (L.). *F Neofiber alleni* True. *G Deomys ferrugineus* Thomas. *H Gerbillus pyramidum* Is. Geoffr. *I Meriones melanurus* Rüppell. *K Psammomys obesus* Cretzschm. *L, M Hydromys chrysogaster* E. Geoffr. *N Ctenodactylus gundi* (Pall.). *O Hystrix cristata* L. *P Dasyprocta aguti* (L.). *R Hydrochoerus capybara* (Erxl.). *S Coelogenys paca* L. *T Dolichotis patagonica* (Shaw). *U Chinchilla velligera* Prell. *V Myocastor coypus* (Mol.).

may show a characteristic deviation in which the papilla is long and projects into the ureter. This is the case in some forms living in deserts, namely *Gerbillus*, *Meriones* (fig. 10 *H*, *I*), *Dipodomys*, *Jaculus*, *Psammomys* (fig. 7 *E—H*), *Ctenodactylus* (fig. 10 *N*), and *Hapalotis*. *Mus musculus* (p. 304) also shows this feature, but not in such an extreme form as the above-mentioned genera.

It seems quite clear that the simple kidney is the primitive form in the *Rodentia*, as the types showing deviating kidney forms are all relatively large or adapted to amphibious life. In most rodents the medulla is divided into zones, but this is often indistinguishable in preserved material. *Castor* and *Hystrix* show no such differentiation, and probably it is lacking in *Aplodontia*, *Hydrochoerus*, and *Coelogenys* also, and perhaps in *Dasyprocta* and *Myocastor*. In all these the undifferentiated condition is probably secondary.

Carnivora fissipedia.

Felis catus L.

Material. The kidneys of several specimens.

Form. The surface is grooved; in the grooves there are veins (fig. 11 *B*). Cortex and medulla are undivided and the latter forms a low papilla. The latter is distinct in young specimens (fig. 11 *C*), but in old males it is not prominent at all, and thus crest-like (fig. 11 *A*). The area cribrosa is always oblong (about 3—4 mm long and 1.5 mm broad) and lies on the apex of the papilla. Dimensions in mm:

	Weight of one kidney, gm	Dimensions, mm	Cortex, mm	Out. zone, mm	Inn. zone, mm
Young, 12 days	3.25	23×17×15	2.0	3	7
Young female	6.6	30×23×19	3.2	3.1	10
Young female	9.8	33×25×20	3.5	4	10
Female	11	38×25×18	5	4	11
Male	15.5	44×29×21	5.5	4	10.5
Male	17	44×32×23	6	4.5	10.5

In "Male 15.5 gm" the proportions of the volumes of the cortex and the medullary zones has been estimated at: cortex 77 %, outer zone 17 %, inner zone 6 %. (Hollatz 1922 found 70, 23, 7 % resp.).

The tubules. These have been described in detail by Peter (1909). My findings usually agree with his description (cf. also fig. 12 *A*). The

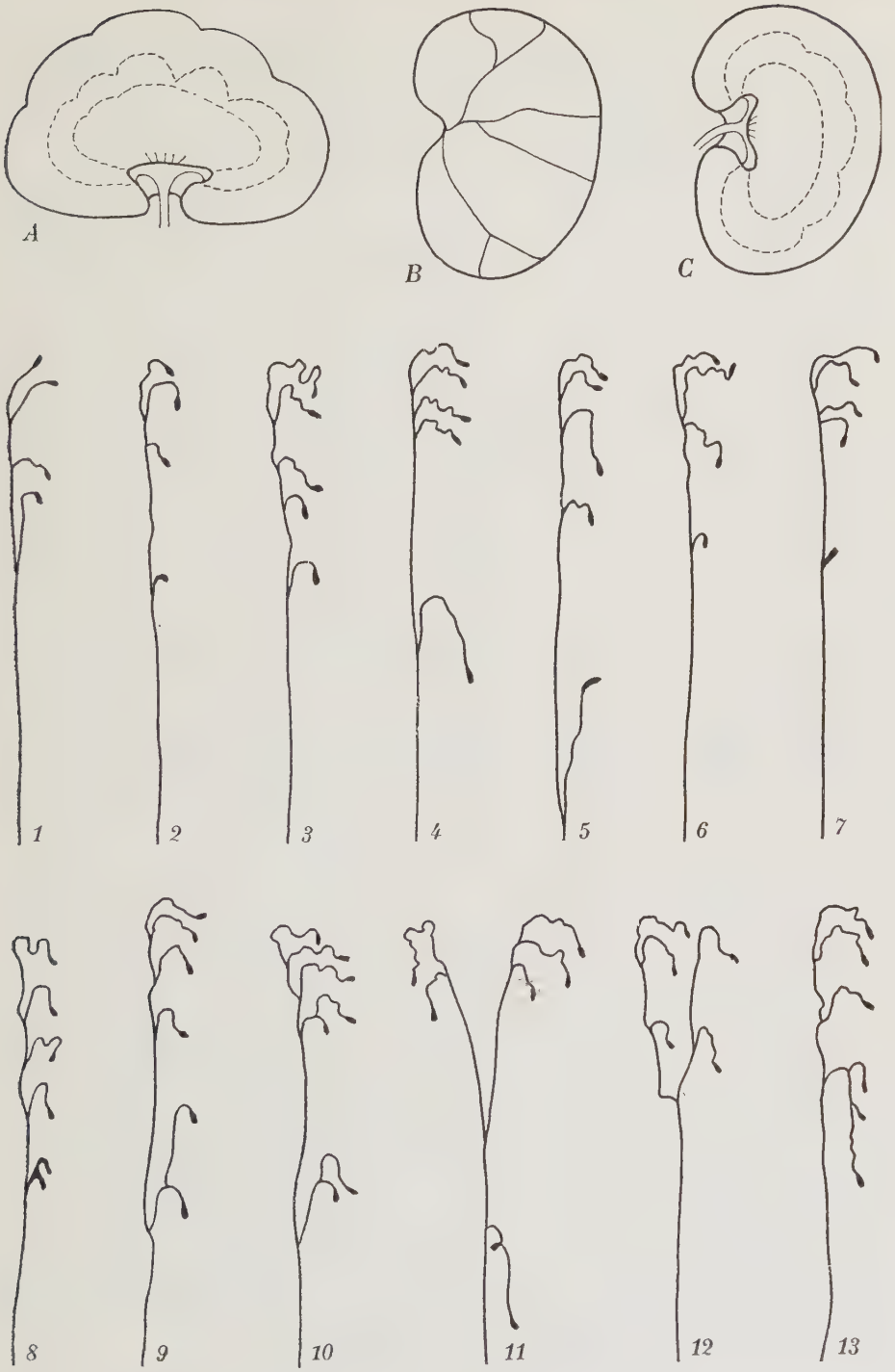


Fig. 11. *Felis catus* L. *A* kidney of "Male 15.5 gm". *B*, *C* kidney of "Female 9.8 gm". *1—13* collecting tubules, (beginnings of distal tubules drawn thick). 15 ×.

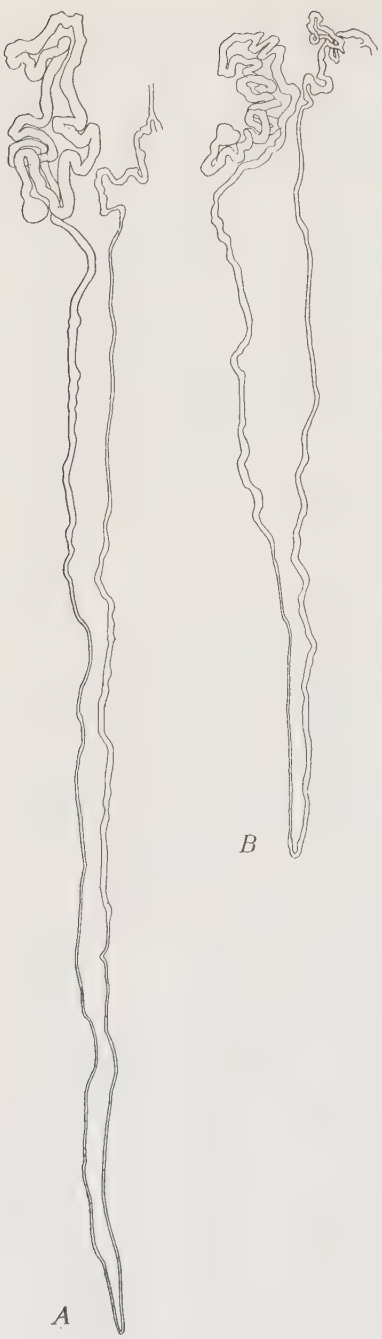


Fig. 12. Nephrons of *A Felis catus* L. 20 ×, *B Lutra lutra* (L.) 20 ×.

proximal tubule is usually fat-laden, except the terminal segment. The latter is almost always markedly thicker than the preceding part. Sometimes the proximal tubule contains little or no fat, or the terminal segment is indistinct. Usually there are long loops only, but in some specimens a very few short loops have been found. The forms of the collecting tubules are shown in fig. 11: *1—13*.

In "Male 17 gm" a number of thin segments have been measured. The average lengths of this specimen are: Proximal tubule 18 mm (corrected for a swelling of about 20 %), 47 %, thin segment 8 mm, 21 %, thick segment 9 mm, 24 % and distal tubule 2.9 mm, 8 %. In "Young female 6.6 gm" the thin segment seems to be at least 5 mm long. The composition of the average tubule is then about 34 %, 30 %, 27 %, 9 % resp. The great difference between the two specimens is certainly not entirely due to errors of estimation, but more probably connected with a very great number of fat-drops in the proximal tubules of the old male.

The cat kidney has been investigated by several authors. The descriptions usually agree with my findings. Zimmermann (1937) states that there are tubi maximi. To prove this he gives a photograph of a section. As no tubi maximi are shown on this, the statement is probably due to some mistake. Marschner (1937) calls the superficial fields, limited by the grooves, 'lobes'. There is little reason for this, and it is apt to cause confusion.

The differentiation of the proximal tubule into a proximal and a terminal segment has been investigated repeatedly (cf. the dog).

Table 26 a. *Felis catus, young, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	85× 75	1200×23	1050× 9	1650×17	550×20	27	24	37	12	4.3
h	90× 75	1400×25	1200× 9	1800×16	600×22	28	24	36	12	5.2
h	85× 68	1550×25	1100×11	1900×15	600×25	30	21	37	12	6.7
h	90× 70	1650×26	1300× 9	1900×16	650	30	24	35	12	6.8
m	90× 70	1900×30	1500×10	2250×17	600×26	30	24	36	10	9.0
m	94× 75	2000×33	1950×11	2700×16	800×23	27	26	36	11	9.4
m	95× 80	2300×39	2200×10	2800×18	900×23	28	27	34	11	10.0
d	110×105	2600×35	4400×13	3100×21	900×35	24	40	28	8	7.6
d	115× 95	4000×38	5800×12	3000×21	1000×34	29	43	22	6	13.9
d	180×135	5800×40	8000×14	3000×20	750×35	33	46	17	4	9.5
Mean	94	2440×31 ±450	2850×11	2410×18 ±180	735×27					8.2

Table 26 b. *Felis catus, young female, kidney weight 6.6 gm, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Ind.
h	105× 90	5000×44		4900		23.3
m	135×115	5200×50		4500		16.7
m	135× 90	5200×43		4500×23	1500×30	18.4
h	120×120	5300×44		4800		16.2
h	115×110	5400×42		4900		17.9
h	130×105	5400×46		5300×21	1600×28	18.2
h	135×110	5500×49		5000		18.1
h	130×100	5600×45		5000		19.4
m	150×115	5800×46		4200		15.5
m	150×135	6000×45		4600×22	1500×30	13.3
m	155×130	6100×44		4000		13.3
d	175×125	6150×51		3100×28	1600×34	14.3
h	190×120	6400×46		4700×24	1800×32	13.9
m	150×130	6500×48		4600×23	1400×33	16.0
d	190×170	7800×52		2800×29	2000×30	12.6
Mean	131	5823×46 ±180		4460×24 ±160	1629×31	16.5

Table 26 c. *Felis catus, young female, kidney weight 9.8 gm, tubule dimensions in μ.*

Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
195×185	7800×54	11.7		200×200	8600×54	11.6
	8000×57			230×185	9200×57	12.3
	8200×46			250×230	9900×58	10.0
240×185	8600×53	10.2		230×185	10400×56	13.7
			Mean	210	8838×54	11.6

Table 26 d. *Felis catus, young female, tubule dimensions in μ.*

Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
154×119	8200×50	22.4		150×125	11100×55	32.6
152×125	9600×51	25.8		150×145	11300×52	27.0
186×133	10900×53	23.4		180×146	12800×53	25.8
			Mean[1]	152	11038×53	25.9

Table 26 e. *Felis catus, female, kidney weight 11 gm, tubule dimensions in μ.*

Capsule	Prox. tubule	Ind.	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
165×165	7500×70	19.3	210×145	8300×71	19.4		190×160	8800×63	18.2
185×150	7600×63	17.3	190×170	8400×64	16.6		170×150	9100×67	23.9
175×160	8000×71	20.3	175×170	8400×64	18.1		210×150	9400×69	20.6
190×165	8200×72	18.8	165×165	8600×62	19.6	Mean[1]	171	8469×66 ±130	19.4
190×165	8300×67	17.7	195×150	8700×68	19.1				

Table 26 f. *Felis catus, female, kidney weight 13 gm, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
		8100×50	
	210×205	8600×55	11.0
	220×175	9800×54	13.7
	230×205	10000×55	11.7
		13000×53	
Mean	208	9900×53	12.1

[1] Including the data of table 26 k.

Table 26 g. *Felis catus, male, kidney weight 15.5 gm, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
	225×225	10500×75	15.6		253×203	12000×71	16.6
	248×210	11300×73	15.8		248×248	12400×75	15.1
	248×203	11700×75	17.4		278×195	12400×74	16.9
	240×233	11800×76	16.0		270×248	14000×77	16.1
	240×220	11800×72	16.1		300×300	15300×75	12.8
	225×220	12000×74	17.9	Mean	240	12290×74 ±400	16.0

Table 26 h. *Felis catus, male, kidney weight 17 gm, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
h	300×225	20300×110	33.1
m	285×210	22000×115	42.3
d	195×195	22500×115	68.0
h	225×190	23800×120	66.8
Mean	228	22150×115	52.6

Table 26 i. *Felis catus, male, kidney weight 20 gm, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
	195×195	13900×69	25.2
	190×190	14700×72	29.3
	210×195	16800×75	30.8
	260×190	18800×74	28.2
Mean	203	16050×73	28.4

Table 26 k. *Felis catus, young female* (1) *and female, kidney weight 11 gm* (2), *tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s	th. s.	d. t.	
(1) *h*	200×170	11700×56	5500×15	7000×25	2000×31	45	21	27	8	19.3
(1) *m*	150×150	12700×54	6300×17	5700×28	1800×30	48	24	22	7	30.5
(2) *h*	190×130	8300×61	6500×12	4700×29						20.5
(2) *h*	165×165	8900×65	7300×14	4600×28	1300×31	40	33	21	6	21.2
(2) *h*		9000×62	5100×11	4700×30	1200×37	45	26	24	6	

Table 27. *Arctitis binturong, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p.t.	t.s.	th.s.	d.t	
hc	110×110	3500×29	0	1900×15	1100×18	54	0	29	17	8.4
hc	100× 95	3700×28	50×5	2100×14	1000×15	54	1	31	15	10.9
h	90× 90	3800×30								14.1
m	95× 90	4800×31								17.4
m	115× 90	5100×29								14.3
d	115× 90	5200×31	1500×6	3700×16	900×20	46	13	33	8	15.6
d	115× 75	5800×24		3800×16	1200×15					16.1
m	110×105	6000×30	500×7	2900×16	1800×18	54	4	26	16	15.6
dd		(5800)	(4500)	(3800)	(1200)	(38)	(29)	(25)	(8)	
Mean	100	4738×29	6	2880×15	1200×17					14.1

Arctitis binturong Raffl.

Material. One pair of kidneys in alcohol.

Form. The kidneys are oblong, 37 × 20 × 12.5 mm. The cortex is relatively thick, about 5 mm, the medulla undivided, about 7 mm. The papilla is low and the area cribrosa oblong (fig. 14 *B*, p. 334); thus the former represents a transitional type between a common papilla and a crest.

The tubules. There are cortical nephrons, but no typical long loops. The epithelium of the capsule is often high and opaque where the proximal tubule emerges. The proximal tubules are highly tortuous and always have a well-developed pars recta. It is not possible to distinguish structurally a terminal part. The cortical nephrons often have no thin segment. The loops turn in the thick segment, except in the deepest nephrons, in which the bend lies within the thin segment. It might thus be permissible to speak of long loops, but the ascending part of the thin segment is very short. The thick segment is normally divided into a thicker and a thinner part, but the difference is slight and may be entirely absent both in deep and high nephrons. The distal tubule is of the common type and the initial collecting tubule is often absent. The collecting tubules normally have well-developed arcades. The central junctions most often occur in the medulla, but there may be some in the inner parts of the cortex, too.

After maceration there is a shrinkage of about a third of the initial dimensions.

Canis familiaris. L.

Material. One pair of kidneys.

Form. Dimensions: Right kidney 54 × 37 × 31 mm, left kidney 53 × 36 × 30 mm. Weight 34 gm and 33 gm respectively. The medulla forms a short crest, and the area cribrosa is about 10 mm long. At the extremities of the latter there are two recesses, about 2 mm deep (fig. 13 *A*). Several collecting ducts open into these recesses. The pelvis has

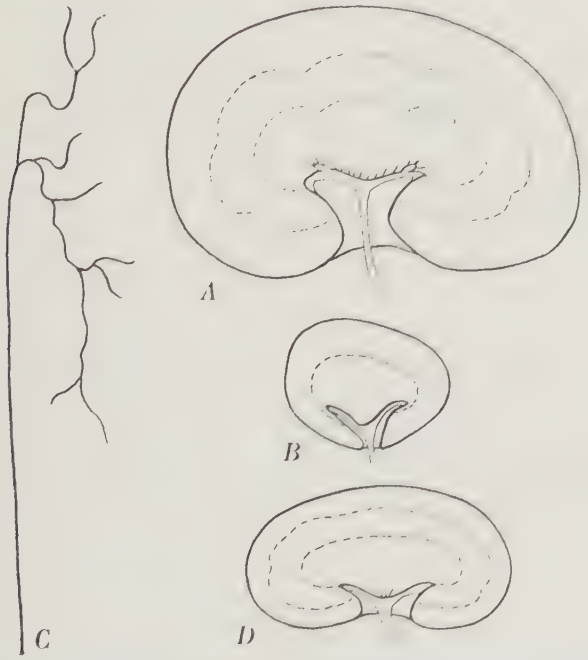


Fig. 13. *A* kidney of *Canis familiaris* L. *B* renculus, *Ursus arctos* L. *C* collecting tubule, *Ursus arctos* L. *D* kidney of *Mystela erminea* L. 2 ×.

well-developed processes. The cortico-medullary boundary is distinct but wavy (fig. 13 *A*). The cortex is 6.5—7.5 mm thick, the outer zone about 6 mm (outer stripe about 3 mm), the inner zone 10—11 mm.

The tubules. There are only long loops. The shape of the capsule varies, but roundish types are most common. There is usually a distinct neck, which is, in some cases, up to 0.15 mm long. The proximal tubules consist of two parts. The first of these mainly occupies the convoluted portion and has a uniform, relatively small diameter (about 0.045 mm). The terminal segment is considerably thicker at its beginning (up to 0.08 mm), but gradually narrows. The transition is gradual, and in the specimen examined by me the structure is relatively uniform

throughout the proximal tubule. The transition into the thin segment occurs at different levels, but always in the outer stripe. The proximal tubules of the deepest nephrons end most centrally. The epithelium of the thin segment is extraordinarily low and transparent. All loops turn in this segment, but in the highest nephrons its ascending part is short, since their loops turn quite near the zone boundary. The thick segment is distinctly differentiated into a thicker and a thinner part. The latter is only about 0.020 mm thick, and its cells are low and transparent. The distal tubule consists of distinct segments. The first of these is the intercalated segment, which is sometimes absent. The next portion is thick and opaque (Pl. 3, fig. *3*). It narrows gradually, becomes more transparent, and passes into a part which is perhaps best referred to the initial collecting tubule. It is thin and light, and is provided with small hemispherical protuberances. Then follows, in some cases, the initial collecting tubule proper, which has no such protuberances, but is otherwise quite like the segment last mentioned. The collecting tubules may show the same types as those of the cat (cf. fig. 11, p. 319). They are thin and transparent, except in the innermost parts of the medulla. Since the collecting tubules are thin (mainly about 0.020 mm thick) a relatively large part of the inner zone is occupied by thin segments.

In addition to the measurements of table 28 the following proximal tubules have been measured: High 15.6, 15.7 and 16.1 mm, middle 13.6, 14.5 and 15.3 mm, deep 13.2 and 13.6 mm long. The mean length is then 14.78 $\pm$ 0.25 mm. The mean length of the thin segment has been estimated from a portion of the medulla containing 49 loops. The mean is about 10 mm. The thick segment has been measured in 12 further nephrons, and its mean length is 8.3 $\pm$ 0.28 mm; the mean length of the distal tubule is 3.2 mm. The composition of an average nephron may thus be estimated at: Proximal tubule 41 %, thin segment 27 %, thick segment 23 %, distal tubule 9 %.

The macroscopical structure of the dog kidney has been investigated by several authors. Their results are usually entirely in accordance with my findings. The tubules have been examined by Peter (1909), who gives some statements on the structure of the proximal tubule and the loops. Foote and Grafflin (1938) have given data as to the length and structure of the proximal tubule and its terminal part. These authors find the terminal segment distinguished by the epithelium containing numerous refractive drops. This agrees with statements by other authors, and certainly represents the common condition. Further statements concerning the structure of the proximal tubule are given by Schachowa (1876), Zimmermann (1911), Nakamura (1935), Foote (1936), and Grafflin and Foote (1938).

Table 28. *Canis familiaris, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
d	240×145	12800×53		5500						19.5
d	190×180	13100×54								20.7
m	210×190	13200×58								19.2
d	220×195	13500×56								17.6
d		13500×58		5500×32	3500×36					
d	260×170	13700×56	15000×18	6000×35	3900×40	35	39	16	10	17.4
h	180×175	14200×55	5200×12	9500×32	3000×35	45	16	30	9	24.8
h	195×170	14600×56	6400×15	10200×36	3200×40	42	19	30	9	24.7
d		14800×60	18							
h	235×160	15400×60	9000×16	8600×35	3300×40	42	25	24	9	24.6
h	205×165	15600×53	8000×14	9300×31	3300×39	43	22	26	9	24.4
h		15900×55								
m	195×195	16000×56								23.6
h	250×180	16100×55								19.7
h	250×240	16500×54								14.9
h	190×165	16500×53		8800×33	3700×38					28.8
h	180×160	16500×54	6700×15	9500×34	3600×31	45	18	26	10	30.9
dd		(15000)	(24000)	(5500)	(3500)	(31)	(50)	(11)	(7)	
Mean	196	14818×56	15	34	37					22.2

Ursus arctos L.

Material. Several pairs of kidneys in alcohol.

Form. The bear kidney is composed of typical renculi, which are held together chiefly by the branches of the ureter and the blood-vessels. In one kidney, which has later been macerated, there are 34 renculi. The dimensions are 95 × 65 × 45 mm, and the dimensions of the renculi are on an average 20 mm. The cortex is 4.0—4.5 mm thick, and the medulla 7—9 mm. The zones are indistinguishable, but after maceration the outer zone is 4 mm and the inner zone 4.5 mm thick. Each renculus has a small pointed papilla (fig. 13 *B*, p. 325).

The tubules. The capsule usually lies central to the convolutions of the proximal tubule. In the deepest nephrons the capsule thus lies at or below the cortico-medullary boundary. The proximal tubules are thickest at the beginning and narrow gradually until they broaden abruptly some way from the transition into the thin segment. The terminal segment then

narrows continually towards this transition, which occurs at varying levels: in the highest nephrons at the cortico-medullary boundary and in the deepest ones some 1.5 mm below this. There is always a thin segment. The loops of the highest nephrons turn at the stripe boundary and most often within the thick segment. The difference between the thicker and the thinner part of the thick segment is indistinct, especially in the deepest nephrons. The distal tubule has about the same diameter as the thick segment, and is tortuous with an irregular contour. There is normally an initial collecting tubule. The collecting tubules are mostly formed by an arcade with 4 adjoining nephrons, one or two nephrons joining it where it turns towards the medulla (fig. 13 *C*).

48 short and 10 long loops have been counted.

It is, of course, difficult to estimate the average composition of a nephron on the basis of this material. The mean lengths of the proximal tubule and the thick segment as given in the table may be accepted as the means of the alcohol kidney. As the proximal tubule forms about 50 % of the nephron length both in high and deep nephrons this figure must apply to the average nephron also. The thin segment constitutes

Table 29. *Ursus arctos, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	150×130	8800×43	1300×15	5000×27	2200×32	51	8	29	13	19.4
d	150×150	9000×46								18.4
h	160×145	9800×44								18.6
h	160×135	10100×42								19.6
m	165×135	10200×51	2700	5400	2500×30	49	13	26	12	23.4
h	175×140	10500×45	1400×13	5500×30	3600×28	49	7	26	17	19.3
h	165×150	10500×40								17.0
d	160×150	10600×46		5000×33	2000×31					20.3
h	175×130	10900×48								23.0
m	180×130	11000×49	2700×12	6000×29	1800×30	51	13	28	9	23.0
m	165×165	11300×50	2500×14	5400×30	2300×34	53	12	25	11	20.8
m	190×165	11700×52								19.4
m	215×155	12800×47								18.1
d	195×165	13100×48		3800×33	2200×35					19.5
dd	210×190	16500×53	(11000)	(3800)	(2200)	(49)	(33)	(11)	(7)	21.9
Mean	162	11120×47 ±490	14	5157×30	2371×31					20.1

about 10 % of the total length in high and middle nephrons. In deep nephrons the percentage may rise to 30—35, and is probably not over 25 on an average. The average percentage of the thin segment may be estimated at 13—15. As the thick segment is usually somewhat more than twice as long as the distal tubule, the former is probably about 25 % and the latter about 11 % of the nephron length.

Mustela erminea L.

Material. The kidneys of three males.

Form. The kidney weight is about 1.5 gm, and the dimensions about 18 × 9 × 8 mm. The surface is even. The papilla is somewhat oblong and low (fig. 13 *D*, p. 325), but the area cribrosa is small and nearly round. The pelvis has distinct processes. The cortico-medullary boundary is even, or slightly wavy. The zone boundary is even and distinct. The cortex is about 1.5 mm thick, the outer zone about 1.7 mm, the inner zone 4.0—4.5 mm. The outer stripe is distinct only after maceration, 0.5—0.6 mm thick.

The tubules. There are few short loops and numerous long loops. The capsule is round or nearly round, with few exceptions. There is seldom a neck. The last portion of the proximal tubule is slightly thinner than the preceding part in two of the specimens investigated, but in the third the first part of this portion is thicker than the part immediately preceding it. It has not been possible to find any certain structural differentiation between the portions of the proximal tubule. The pars recta is very short in the deepest nephrons, and it narrows abruptly at the transition into the thin segment in all nephrons. The loops turn in the thin segment, which makes it difficult to distinguish between short and long loops. The short loops turn near the zone boundary. The relation between short and long loops has not been accurately determined, since these last two circumstances make it nearly impossible to do so. It is, however, quite certain that the long loops are far more numerous than the short. The thick segment is always differentiated into a thicker and a thinner part. The latter is long and narrow in the high nephrons, but relatively broad and indistinctly differentiated in the deep nephrons. The distal tubule has an irregular contour and often shows some small projections. The collecting tubules often possess small arcades. Their central junctions occur in the inner zone. The collecting tubules are thin except in the innermost parts of the medulla.

The means of the table may be accepted as the true means, as there is probably no marked over-representation of the deep nephrons.

Table 30. *Mustela erminea, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
m	98× 95	3300×39	2900×10	2300×24	1050×25	35	30	24	11	13.8
h	105× 90	3400×38	1400× 8	2600×23	1000×25	40	17	31	12	13.7
h	100× 90	3400×38								14.4
h	103× 90	3500×39	1400× 9	2300×22	1100×26	42	17	28	13	14.7
m	110× 80	3500×38								15.1
h	90× 86	3600×40	2300× 9	2400×25	1200×25	38	24	25	13	18.6
h	115× 94	3700×42								14.4
m	115× 95	3800×41	3100×10	2300×24						14.3
h	105× 90	4000×35	1000×10	3000×27	900×31	45	11	33	10	14.8
m	108×105	4100×39	2200×10	2300×26	1200×26	42	22	23	12	14.1
m	113× 85	4500×40	4400× 8	2300×27	1400×28	36	35	18	11	18.7
d	133×105	4900×45	·	2100×28						15.8
dd[1]		6200	(9000)	(2000)	(2000)	(32)	(47)	(11)	(11)	
Mean	100	3808×39.5 ±140	9	2400×25 ±90	27					15.2

Lutreola vison (Schreb.).

Material. The kidneys of a large male.

Form. The kidneys in most respects resemble those of *Mustela*, but the papilla is lower still (fig. 14 *L*, p. 334). The dimensions of the right kidney are 36 × 20 × 16 mm and the weight 6.3 gm. The corresponding figures for the left kidney are 36 × 20 × 17.5 mm and 6.8 gm. The cortico-medullary boundary is distinct and wavy. The cortex is about 3.5 mm thick, the outer zone 3.0—3.5 mm, the inner zone 7.0 mm. The area cribrosa is small, and concentrated at the apex of the papilla. The pelvis has processes. Both the ventral and the dorsal surface of the kidney are covered by the peritoneum.

The tubules. These are very like those of *Mustela erminea*. The terminal part of the proximal tubule is distinctly thicker and more opaque than the preceding part. The thick segment is differentiated into a thicker and a thinner part. The short loops agree with those of *Mustela* and are relatively few — 27 short and 78 long loops have been counted. The dimensions of some nephrons are given below.

[1] The deepest proximal tubule has been measured in another kidney of similar size, and is not included in the mean.

Table 31. *Lutreola vison, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	165×155	6200×45	2500×11	3900×30	1900×35	38	15	36	12	10.9
m	185×185	7700×50		5200×35	2300×36					11.2
m	185×150	8000×50								14.4
h	195×195	8600×52	2300×12	6600	2900	42	11	32	14	11.8
h	196×184	9000×50								12.5
m	230×195	9200×50								10.3
h	215×190	9400×58								13.3
h	210×195	9700×50								11.8
d	215×185	10000×54								13.6
d	230×205	11000×54								12.6
dd	240×240	12200×57	(15500)	3200×24	3500×34	(35)	(45)	(9)	(10)	12.1
Mean	198	9182×52 ±490	12	30	35					12.2

Lutra lutra (L.).

Material. The kidneys of an old female and a young male. They had been kept in weak formaldehyde solution for a short while before I had the opportunity of examining them, but as the solution had penetrated only into the outer layers, it is improbable that the dimensions had been altered to any significant extent.

Form. The weight of the kidneys of the female is 52 gm, and that of the male 34 gm; the dimensions of one kidney are 67 × 29 × 29 mm, and 64.5 × 23.5 × 21 mm respectively. In the former kidney there are 11 renculi, in the latter 13. Each renculus has a pointed papilla, and there are processes emerging from the pelvis of the renculus, which is itself a branch of the pelvis of the kidney. The cortex is 3.0—3.5 mm thick, the outer zone 3—4 mm, the inner zone 6—8 mm.

The tubules. The proximal tubules show no differentiation of the terminal part comparable to that occurring in the cat and the dog, but this part is usually slightly more slender than the main part of the proximal tubule (fig. 12 *B*, p. 320). The transition into the thin segment is gradual, and occurs at the same level in all nephrons. The short loops most often turn within the thick segment, and their apices normally lie a short distance peripheral to the zone boundary. The thick segment is differentiated into a thicker and a thinner part. The distal

Table 32 a. *Lutra lutra, female, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
h	180×145	6300×43	10.4	*m*	170×160	7600×45	12.6
h	190×135	6400×43	10.7	*h*	200×150	7700×44	11.3
m	170×160	7100×44	11.5	*m*	173×165	7800×40	10.9
h	180×150	7300×47	12.7	*d*	170×170	8100×44	12.3
h	188×150	7500×45	12.0	*m*	165×150	8200×46	15.2
h	180×150	7500×43	11.9	Mean	166	7409×44 ±160	12.0

Table 32 b. *Lutra lutra, male, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
m	160×150	6000×45	11.3
d	165×135	6600×51	15.1
h	158×143	6800×50	15.0
h	165×143	6900×49	14.3
h	158×113	7300×48	19.6
h	165×150	7400×45	13.5
Mean	150	6833×48	14.8

Table 32 c. *Lutra lutra, female* (1) *and male* (2), *tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %			
						p. t.	t. s.	th. s.	d. t.
(1) *h*	180×150	7300×47	2400×10	5200×27	1500×35	45	15	32	9
(1) *m*	165×150	8200×46	4000×11	5200×30	1700×34	43	21	27	9
(1) *dd*		(8200)	(15000)	(4000)	(1700)	(28)	(52)	(14)	(6)
(2) *h*	165×150	7400×45	1900×11	5200×30	2000×32	45	12	32	12
(2) *m*	160×150	6000×45	3800×10	3600×26	1300×35	41	26	24	9

tubule is irregularly bent and its diameter varies (fig. 12 *B*). The initial collecting tubule is short in most cases. Arcades are seldom found, and are short. In the male the long loops constitute 46 ± 4.3 % of the total number.

The kidneys of *Lutra* have been examined macroscopically by several

authors. The number of renculi normally given is about 10—12 (Milne-Edwards 1862, Gerhardt 1914, Anthony 1922, cited according to Freund 1939). I, too, have found this number in some alcohol specimens, in addition to those described above[1].

Carnivora fissipedia, survey of the form of the kidney.

All *Viverridae* investigated have simple kidneys with one papilla. The papilla may be very low and crest-like, as in *Arctitis* and *Crossarchus obscurus* F. Cuv. (Gerhardt 1914). In this case the area cribrosa is lengthened as compared with the area cribrosa in forms with a more prominent papilla. Such forms are *Cryptoprocta ferox* Benn. (fig. 14 *C*), *Prionodon linsang* (Hardw.) (fig. 14 *D*) and *Viverra sp.* (fig. 14 *A*), examined by me, and *Viverra zibetha* L., *Paradoxurus hermaphrodyta* Schreb., *Suricata tetradactyla* Schreb., *Nandinia binotata* (Reinw.), *Genetta tigrina* (Schreb.), *Herpestes ichneumon* (L.) — all according to Gerhardt (1914). The pelvis has processes in *Viverra* and *Herpestes* (Hyrtl 1872). There are some branching veins on the surface of the kidney of *Herpestes griseus* (Inouye 1931, p. 99), and this is probably the case in other species, too. They are, however, difficult to see in preserved material.

Hyaena has been investigated by Hyrtl (1872), Gerhardt (1914) and the author. There is a typical short crest (fig. 14 *E*). The area cribrosa in my specimen lies in a shallow groove in the crest; this groove is slightly deeper at the one extremity. The pelvis has well-developed processes, and the surface of the kidney is grooved by veins.

The kidneys of the *Felidae* are of fairly uniform structure. The surface shows richly arborescent veins, and the pelvis has processes (cf. especially Hyrtl 1872). The medulla forms either a papilla or a short crest. There is no clear difference between the papilla shown by the kidney of a young cat, for example, and the short crest in the kidney of an old cat or the larger *Felidae* (fig. 11 *A*, p. 319). In both cases the area cribrosa is oblong, but not so long as in most kidneys with a crest. In the cat the form of the papilla seems to depend on the age of the specimen (cf. fig. 11 and p. 393). This is probably the case with the lion also. Thus, in the young lion examined by me, there is a short papilla (fig. 14 *F*), in the specimen examined by Gerhardt (1914) the papilla is very low, and in a large kidney Hecking (1940) finds a short crest. In *Felis onca* L. and *Lynx* (fig. 14 *G*, *H*) the area cribrosa shows at its extremities small recesses, somewhat reminiscent of those of the dog.

Canis familiaris, *Canis lupus* L. (fig. 14 *I*), *Canis latrans* Say. (Gerhardt 1914), and *Cuon alpinus* Pall. (Gerhardt 1914) have typical short

[1] A young American *Lutra* has about 100 renculi (cf. Kingsley 1917, p. 369).

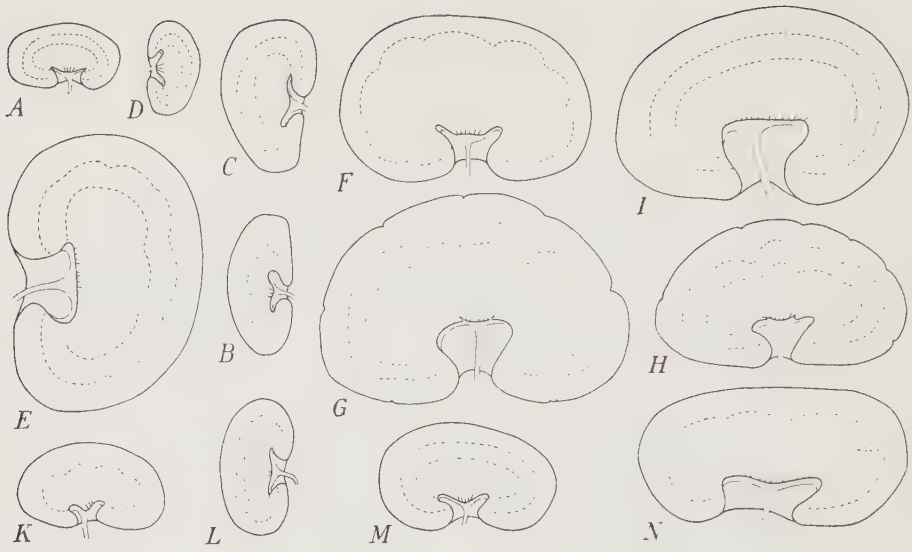


Fig. 14. *Carnivora*, kidneys. 1/2 ×. *A Viverra sp. B Arctitis binturong* Raffl. *C Cryptoprocta ferox* Benn. *D Prionodon linsang* (Hardw.). *E Hyaena sp. F Felis leo* L. pull. *G Felis onca* L. *H Lynx lynx* (L.). *I Canis lupus* L. *K Nasua narica* (L.). *L Lutreola vison* (Schreb.). *M Meles meles* (L.). *N Gulo gulo* (L.).

crests. Gerhardt (1914) does not mention any recesses in the crest, nor have I found any in the wolf kidney. It seems doubtful if there are always such structures in the dog (cf. p. 325), as they are very easily overlooked. Still more doubtful is their morphologic interpretation. They would seem to agree closely with the corresponding structures in the crest of the large *Felidae* and in *Hyaena*, which are only dents in the crest. The tubi maximi, on the other hand, are certainly in most cases enlarged collecting ducts. If this is so it would be rash to rank these recesses with tubi maximi.

In the *Procyonidae Nasua narica* (L.) (Gerhardt 1914; also fig. 14 *K*), and *Potos flavus* Schreb. have a distinct papilla. *Ailurus fulgens* F. Cuv. has a crest-like papilla (Gerhardt 1914), and *Procyon cancrivorus* G. Cuv. (Gerhardt 1914) and *Procyon lotor* (L.) have a crest. As Gerhardt points out, the smaller species have a papilla and the larger ones a crest.

Ailuropoda, the systematic position of which is somewhat uncertain, but which is often referred to *Procyonidae*, has kidneys divided into six lobes (Raven 1936).

All bears have renculi-kidneys. Examined are: *Ursus arctos* (several authors), and, according to Gerhardt (1914), *Ursus isabellinus* Horsf., *Ursus malayanus* Raffl. and *Melursus ursinus* Shaw.

Among the *Mustelidae* there is a papilla in the following forms: *Mustela* (cf. also Gerhardt 1914), *Martes martes* (L.) and *Lutreola vison*

(Schreb.). GERHARDT states that *Lutreola lutreola* (L.) has a crest, but it seems more probable to me that there is in this species, as in *L. vison*, a low, crest-like papilla. *Gulo* (GERHARDT 1914; also fig. 14 *N*) and *Galictis barbara* (L.) (GERHARDT 1914) have a crest. GERHARDT (1914) states that *Meles meles* (L.) shows the papilla divided into two parts, each with an area cribrosa. In a specimen examined by me the papilla is low, and the area cribrosa is oblong; it thus shows an intermediate state between papilla and crest (fig. 14 *M*). *Lutra* has renculi-kidneys, as has *Latax* (106 renculi, STELLER 1753).

From this survey it is evident that all small carnivores have kidneys with a papilla. Most of the other forms have kidneys with a crest, or transitional forms towards such. In respect of this, it is clear that the lobulated kidneys of the bears and the otters have developed independently. If it is assumed that *Ailuropoda* is a close relation of the bears, it may be supposed that the lobation of its kidneys is a feature developed in connection with the lobation of the bear kidneys. It seems, however, more likely that the lobation of the *Ailuropoda* kidney has developed independently, and if *Ailuropoda* is considered more allied to the *Procyonidae* this must be the case.

The medulla of the kidney in *Carnivora* is usually divided into zones. *Arctitis* has no distinct inner zone, and in the bear kidney it is relatively low. In the lion kidney, on the other hand, the inner zone is unusually thick.

Carnivora pinnipedia.

Phoca hispida Schreb.

Material. One pair of fresh kidneys, which have been macerated, and several kidneys in alcohol.

Form. The fresh kidneys weigh 130 gm and 113 gm. The dimensions are 119 × 56 × 37 mm, and 113 × 58 × 31 mm. The kidneys are surrounded by a layer of tough connective tissue. When this has been removed a large number of renculi are seen on the surface of the kidney (Pl. 2, fig. *4*). The surface of each renculus shows a number of arborescent veins. The boundaries of the renculi are distinct only on the surface of the kidney, as the connective tissue uniting them is poorly developed. This does not mean that there are no boundaries at all, for the nephrons of each renculus lie exclusively between nephrons of the same renculus, touching nephrons of the other renculi only at the renculus surface. Each renculus also has blood-vessels of its own, with the exception that the veins of the surface may be joined by small veins from two neighbouring renculi. Each renculus has, normally, a papilla (fig.

15 *A*, *B*). The pelvis of the renculus, which is only an end branch of the renal pelvis, has no processes.

In one of the kidneys examined there are about 75 renculi reaching the surface of the kidney, and about 10 entirely situated in its interior (fig. 15 *C*). The cortex is of about the same thickness in all renculi, i. e. 2.2 mm. The outer zone is about 3.0 mm thick, the inner zone 5—6 mm.

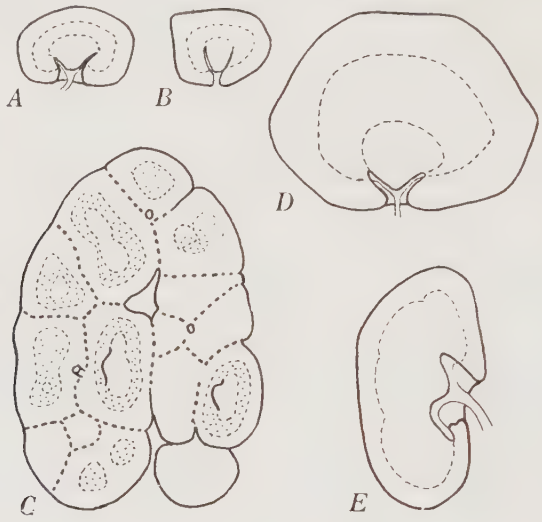


Fig. 15. *A*, *B*, *C* *Phoca hispida* (Schreb.). *A*, *B* renculi, *C* cross section of the kidney, outer zone dotted. *D* *Balaenoptera musculus* (L.), renculus. *E* *Procavia capensis* Pall., kidney.

The cortex constitutes about 72 % of the weight of the kidney, the outer zone about 24 %, the inner zone 4 %.

The tubules. The proximal tubule is divided into a more proximal and a terminal part. The former is thickest at the beginning, and narrows continually. At the beginning the latter is thicker than the last portion of the proximal part, and its diameter diminishes continually until immediately before the transition into the thin segment, which is abrupt. The highest proximal tubules end slightly above the stripe boundary. The highest loops turn as much as 1 mm. above the zone boundary. The bend usually occurs at the transition between thin and thick segment. The latter is always differentiated into a thicker and a thinner part. The initial collecting tubule and the collecting tubule are thin and transparent. The peripheral junctions are direct, normally, but there may be small arcades.

The percentage of long loops is 42 ± 4.5. The terminal segment occupies on an average 28 % of the proximal tubule. The thin segment is on an average 3.5 mm long, the thick segment 3.8 mm (8 more data), the distal tubule 1.0 mm.

Table 33. *Phoca hispida, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
	135×120	4150×42	10.8	*d*	150×135	5200×41	10.5
h	155×124	4400×38	8.7	*d*	153×124	6080×47	15.1
h	140×130	4430×39	9.5	*d*	160×135	6200×43	12.3
h	145×115	4650×39	10.9	*d*	195×140	6230×46	10.5
m	160×150	4750×42	8.3	*d*	165×150	6750×40	10.9
m	135×130	4800×40	10.9				

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
	135×135	4200×40	1300× 6	3750×22	800×30	42	13	37	8	9.2
h	145×105	4730×38	1650× 8	4050×26	900×24	42	15	36	8	11.8
h	140×112	4800×40	1500× 8	4200×25	1200×30	41	13	36	10	12.2
h	150×145	5100×38	1800×10	4050×25	900×30	43	15	34	8	8.9
h	165×135	5550×41	1950×10	4500×23	1150×30	42	15	34	9	10.2
m	190×150	6150×49		4700×26						10.6
d	270×130	6250×41		3380×24	1000×28					7.3
dd		(7000)	(12000)	(3000)	(1200)	(30)	(52)	(13)	(5)	
Mean	146	5245×41 ± 200	8	4090×24	992×29					10.5

Phoca barbata Erxl.

Material. One kidney in alcohol.

Form. The dimensions, 205 × 83 × 53 mm, are much larger than in *Phoca hispida*, but otherwise the agreement is close. After maceration there is a swelling of about 30 %, and then the cortex is 3.6 mm thick, the outer zone 5.5 mm, the inner zone 9 mm. The latter measurement is fairly variable.

The tubules. These also agree in essentials with those of *Ph. hispida*. The proximal tubules end at slightly different levels. The transition between thin and thick segment in long loops occurs at varying levels, too. Thus the zone boundary becomes somewhat indistinct.

The long loops constitute 68 ± 3.4 % of the total number.

Table 34. *Phoca barbata, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	195×195	9500×55	6000×15	8000×33		(34)	(22)	(29)		13.7
h	225×180	9700×60	6700	9400×32		(35)	(24)	(34)		14.4
h	225×195	10000×53								12.1
h	240×195	10000×56	6000	10000×34	2100×38	36	18	36	7	12.0
h	195×195	10800×56								15.9
m	240×205	11600×59								13.9
m	275×240	13500×62		9000×33	2800×36					12.7
Mean	214	10728×57	15	9100×33	37					13.5

Carnivora pinnipedia, survey of the form of the kidney.

The kidneys of the *Pinnipedia* are of very uniform structure. They evidently all belong to the renculi type, though the renculi in mature specimens are closely united, instead of being more loosely connected, as in many other kidneys of this type. Gerhardt (1911, 1914) considers the kidneys of the *Pinnipedia* to be a type distinct from the renculi kidney, but this opinion can hardly hold, as not only embryos but also young specimens show typical renculi kidneys. Accounts of kidneys of this order have been given by Owen (1868), Hyrtl (1872), Chiewitz (1897), Gerhardt (1911, 1914), Anthony and Liouville (1920), Anthony (1922). Anthony and Liouville (1920) state that the kidneys of *Otaria* are only superficially grooved. This is certainly true of mature specimens, but it must be emphasized that the structure of the *Otaria* kidney agrees with that of *Phoca*. This is evident from Gerhardt's account of it (1914), and personal examination of an *Otaria* kidney.

Cetacea.

Phocaena phocaena (L.).

Material. Two pairs of kidneys in alcohol.

Form. The kidneys are composed of renculi, lying in several layers. The renculi are held together by abundant connective tissue. Thus they are easily separated from each other, and there is no tendency to fusion of neighbouring renculi. One kidney in each of the examined pairs has been measured. The dimensions are $105 \times 63 \times 32$ mm and about $140 \times 70 \times 40$ mm. The latter has been macerated, which resulted in

some swelling. After maceration the cortex is 1.7 mm thick, the outer zone 2.4 mm, and the inner zone 3.4 mm.

The tubules. The proximal tubules often begin with a short neck. Their terminal part is not clearly distinguishable, but seems normally to be somewhat slenderer than the preceding part. The short loops turn in the inner part of the outer zone, the highest ones about 0.8 mm from the zone boundary. The bend usually lies at the transition between thick and thin segment. The former has a thicker and a thinner part. The initial collecting tubule is often fairly long. Most peripheral junctions are direct, but there are also small arcades.

The long loops constitute 34 ± 3.5 % of the total number. In addition to the proximal tubules of the table, such measuring 4.3, 4.7 and 5.1 mm have been measured, as also thick segments 3.9, 3.9, 4.0, 4.1 and 4.5 mm long.

My findings agree qualitatively with the description given by Inouye (1909). The percentage of the long loops is also the same. The length of the proximal tubules given by Inouye, 4.7 mm, agrees with the mean length I have found, 5.1 ± 0.25 mm. His figure of the average length of the thick segment, however, is 2.5 mm, which deviates markedly from mine, 4.0 ± 0.1 mm. This great discrepancy is difficult to explain. It may, however, be mentioned that though the drawings of thick segments given by Inouye agree well with his measurements, the two proximal tubules figured by him (op. cit. fig. XIII) are much shorter than any one measured by him. Even if the foreshortening of the loops is taken into account none of them seems to be more than 3.5 mm long. It is possible that differences in shrinkage have occurred between those

Table 35. *Phocaena phocaena, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	160×130	4100×40	1800×12	3700×30	850	39	17	35	8	7.9
h	145×130	4400×43	1600×14	3700	1000×31	41	15	35	9	10.0
h	155×150	4800×45								9.3
m	160×150	4900×47		3800×26	850					9.6
m	180×135	5100×50		3900×28	1200×30					10.5
h	180×150	5500×45								9.2
m	165×165	6000×49								10.8
dd	250×200	7100×60	(8500)	(3400)	(1000)	(36)	(43)	(17)	(5)	8.5
Mean	163	5238×47	13	28	31					9.5

measured and those depicted. But then it seems possible that such differences have occurred between the proximal tubules and the thick segments measured, also.

Balaenoptera musculus (L.).

Material. A piece of a kidney in alcohol.

Form. The kidney consists of renculi, connected by loose connective tissue. The renculi are often slightly flattened. Their dimensions are about $35 \times 30 \times 25$ mm. The pelvis of the renculus is small, without processes. The papilla is small and obtuse (fig. 15 *D*, p. 336). The cortex is about 6 mm thick, the outer zone 9 mm, the inner zone 9 mm. After maceration an outer stripe, about 3 mm thick, is distinguished.

The tubules. The pars convoluta of the proximal tubules is tortuously looped, and the pars recta is always well developed, often slightly looped. The transition into the thin segment occurs at slightly varying levels. The thick segment is strongly differentiated into a thicker and a thinner part. The former is wavily tortuous. The short loops sometimes turn a fairly long distance above the zone boundary. Their bend lies within the thick segment. The distal tubules, and the collecting tubules in this material are very brittle and difficult to isolate. The former seem most often to be about 2 mm long and 0.035 mm thick. Some small arcades have been seen, but most peripheral junctions are direct.

The dimensions of some segments are given below, table 36. 22 long loops and 38 short ones have been counted.

Table 36. *Balaenoptera musculus, tubule dimensions in* μ.

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	190×160	10000×50		10100						16.4
m	230×220	12500×58								15.0
m	220×195	12800×56		12200						16.7
h	220×155	13000×52		11500						19.8
h	230×230	13500×58	7000	12300×38	(2000)	(39)	(20)	(35)	(6)	14.8
d	250×230	15000×60		11500×40						15.7
d	300×210	16000×60		11700						15.2
dd		(16000)	(25000)	(12000)	(3000)	(29)	(45)	(21)	(5)	
Mean	217	13260×56		11550×39						16.2

Cetacea, survey of the form of the kidney.

The kidneys of the *Cetacea* have been investigated by a number of authors. It is clear that all whales have typical renculi kidneys. In addition to the authors cited by Freund (1939), Ommaney (1932) may be mentioned. He has given a thorough account of the structure and development of the kidneys of *Balaenoptera physalus* (L.).

In most whales the renculi are disposed in several layers, and they are very numerous. According to Anthony (1922) *Mesoplodon* has relatively few renculi, all reaching the surface of the kidney.

Hyracoidea.

Procavia capensis Pall.

Material. One pair of kidneys in alcohol.

Form. The dimensions are $30 \times 16 \times 9$ mm and $32 \times 17 \times 9$ mm. The kidney is thus relatively thin, but is otherwise of the common form. There is a well-developed papilla (fig. 15 *E*, p. 336). The pelvis has distinct processes. The cortex is about 2 mm thick, the outer zone about 4 mm and the inner zone about 5 mm.

The tubules. All segments are of the common form. The highest loops turn about 1.2 mm above the zone boundary. The short loops turn in the thick segment. The collecting tubules have small arcades, but most junctions are direct.

After maceration the material had shrunk about 25 %. 62 short and 13 long loops have been counted. The distal tubules are about 0.7 mm long and about 0.030 mm thick.

	Capsule	Prox. tub.	Ind.
m	135×115	6400×30	12.4
h	138×105	6400×32	14.1
m	120×105	7100×29	16.3
h	140×122	7300×32	13.7
m	148×120	7500×34	14.0
Mean	125	6940×31	14.1

Proboscidea.

Elephas maximus L.

Material. The kidneys of a 2-year-old male in alcohol, and the kidneys of a female. The latter have also been examined after maceration.

Form. The kidneys of the male consist of 4 and 5 distinct lobes respectively. The kidneys of the female had been cut into several pieces, and thus it is difficult to be certain as to their form. One of them weighs 2.8 kg, the other 2.35 kg. The dimensions of the latter are about 220 × 190 × 90 mm. It consists of 7 renculi, and the other of 8. In the interior of the kidneys these are distinctly separated by membranes of connective tissue (and probably, as PETTIT (1907) states, smooth musculature too). On the surface they are separated by shallow grooves, here and there indistinct. The ureter and the blood-vessels enter the kidney ventrally. The former branches in the kidney. A branch goes to each renculus, but it has not been possible to ascertain the exact mode of branching. Within the renculus the branch usually ramifies once more, and the end portion of the last branches widens to envelope a very low papilla (fig. 16). The latter is largely occupied by a roundish area cribrosa. On this open several collecting ducts. One of the latter is usually markedly enlarged, and forms a small tubus maximus up to 10 mm long and 1.5 mm wide. Sometimes there are two tubi maximi on the same area cribrosa. Each area cribrosa belongs to a medullary pyramid (fig. 16 *A*, *B*), which is completely separated from the other pyramid in the same renculus by a cortical ridge and by the sinus renculi (fig. 16 *A*). In the smaller kidney with its 7 renculi there are 12 areae cribrosae.

The cortex contains numerous thick medullary rays. It is 15—23 mm thick, and the medulla 15—27 mm. The medulla is not divided into zones, but the innermost part of the medulla is mainly occupied by the wide collecting ducts, and thus shows a more whitish colour. Nor is any inner zone visible after maceration.

The tubules. There are cortical nephrons, but no nephrons with typical long loops. The capsule is of normal appearance, but is often distinctly flattened. The proximal tubule is very tortuous and always has a pars recta, which is relatively short in the deepest nephrons. The thin segment begins at very different levels in the outer zone and the inner parts of the cortex. Thus the outer stripe is not very distinct. It is about 4.5 mm thick. The loops turn everywhere in the medulla and the medullary rays, except in the outermost parts of the cortex. The higher a loop turns, the shorter is its thin segment. The loops of the

deepest nephrons, which turn near the area cribrosa, consist in their deepest part of two limbs of similar structure. The epithelium is very uneven and opaque. This part of the loop must be referred to the thick segment. The transition into the thin segment is, however, very gradual. The difference between the thicker and the thinner part of the thick segment is slight and often absent, especially in the cortical nephrons.

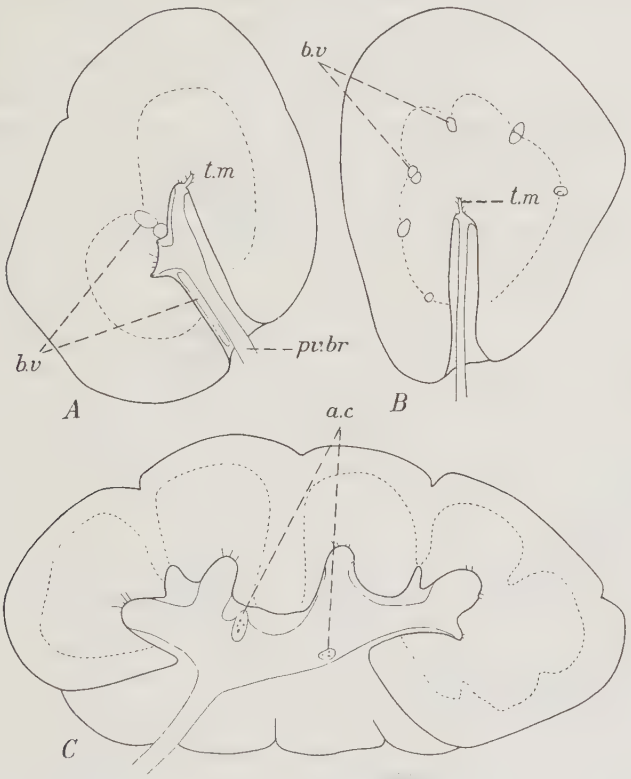


Fig. 16. *A, B Elephas maximus* L., renculi. *b.v* blood-vessel, *pv.br* pelvic branch, *t.m* tubus maximus. $^1/_2 \times$. *C Trichechus manatus* L., kidney. *a.c* area cribrosa. $^1/_2 \times$.

The distal tubule is of the usual appearance. There is usually no initial collecting tubule in the deep nephrons. The collecting tubules are very difficult to examine, as they are very brittle. It is, however, certain that there are arcades, as well as direct junctions. Central junctions occur even in the central parts of the cortex.

The dimensions of some cortical nephrons and proximal tubules are given below, table 37. The longest thin segment I have found is about 10 mm long. The distal tubule is usually about 3.5 mm long. The mean length of the proximal tubules, except those of the cortical nephrons, is about 27 mm. The numerical relation of the cortical nephrons and the

others is not known, and thus the mean length of the proximal tubule cannot be estimated with certainty. This is the case with the other segments, too. Thus, the composition of the average nephron is unknown. It seems clear, however, that the thin segment occupies an unusually small part of it.

The macroscopical structure has been examined by several authors. The majority of the descriptions agree with my findings, but this is often difficult to ascertain, as the terminology varies rather much. Some statements are, however, contrary to my observations. GERHARDT (1911) states that there are, according to DÖNITZ (1872), 4—5 tubi maximi. This is not correct. DÖNITZ states that there are 10 lobes, and tubi maximi, too. FREUND (1939) is aware of GERHARDT's mistake (op. cit. p. 72), but it seems that he himself makes a similar mistake on this same page, when he cites some measurements from HYRTL (1872) as the dimensions

Elephas maximus.

Author	Age	Dimensions in cm	Lobes	Pyramids
WATSON 1873		30×18	5+4	13+10
MIALL & GREENWOOD 1879	young		5+5	2—3 in each lobe
ANDERSSON 1883		26.5×19.5×5.5	8+8	
WATSON 1885			7	
HUNTINGTON 1893	young		6	
PATERSON & DUN 1898	20 years	38×27	6+7	23+27
PETTIT 1908	12 „	30×16.5	5+4	
„ „	14 „	15.5×11.5	6	
FOX 1909	27 „		10	
GERHARDT 1914 (Pl. III, fig. 6)			5	
HAHN 1921			6+6	
„ „			7	
PETIT 1925	7—8 „		8	
SCHULTE 1937	20 „	27.5×22.5	6+7	2—4 in each lobe
BECKMAN 1939	30 „	30×19	6+6	
SPERBER	2 „		4+5	
„		22×19×9	7+8	12
Loxodonta africana.				
HYRTL 1872	4 years		9	9
DÖNITZ 1872			10	
FORBES 1879			8	
v. MOJSISOVICS 1879	2.5 „		10	
PETTIT 1907	30 „		8	
PETIT 1925 (ANTHONY)	foetus		8	

of the tubi maximi. HYRTL's measurements refer to the branches of the pelvis (HYRTL's "calices minores"). On the whole FREUND's survey of the literature is difficult to understand, which is probably due to the fact that he has not examined an elephant kidney himself. This is probably essential to an understanding of the often very obscure descriptions. FREUND (1939) accepts the opinion, first advanced by CAMPER (1803) and later supported by PLATEAU and LIÉNARD (1881) among others, that the number of the renculi diminishes with the age of the individual. PETTIT (1907) and PETIT (1925, p. 59) consider the question open to doubt. On p. 344 I give a table of the statements I have found in the literature on the number of renculi in the elephant kidney, together with my own findings.

The statements by CUVIER (1840) and MAYER (1847) have not been taken into account, as the species is not known. PLATEAU and LIÉNARD (1881) thought there were 5—6 lobes in a part of the kidney they examined; this figure has of course not been included in the survey above (cf. PETIT 1925 and FREUND 1939).

CAMPER (1802, p. 40) says there are 8—9 lobes, but from his figures (Pl. IX, fig. 2, 3) it seems that there are more probably 6 or perhaps 7 renculi, showing varying degrees of subdivision.

This survey certainly gives no support to the theory that the number of renculi diminishes with age. It is, however, clear from the descrip-

Table 37. *Elephas maximus, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
hc	265×220	10100×41	500×15	3500×16						7.1
hc	240×250	10300×50	250×20	3500×22	3700×40	58	1	20	21	8.6
hc	280×280	10300×48	500×17	4900×17	4000×37	52	3	25	20	6.3
hc	275×230	11500×50	350×17							9.1
hc	380×300	18400×60								9.7
m	380×380	20000×62								8.6
d	520×460[1]	26500×63								
d	460×415	27500×60								8.6
m	450×450[1]	28800×63								
d	460×460	29000×58								7.9
Mean	330	19240×56 ±2600	17		39					8.2

[1] Flattened capsules, not included in the mean.

tions in the literature that the furrows may become indistinct in old animals.

The number of renculi in the two kidneys of the same specimen is probably correlated. The mean number of the renculi has been calculated after taking the average number in the individual. This value is 6.35 ± 0.36 in *Elephas*, and 8.83 ± 0.40 in *Loxodonta*. The difference is 2.48 ± 0.54 renculi. The difference is 4.59 times its standard error, and is thus significant, despite the small number of data from *Loxodonta*. Thus it is certain that *Loxodonta* has more renculi than *Elephas*. On the other hand, it is possible that each renculus in *Loxodonta* has only one pyramid, as was the case in HYRTL's specimen, whereas *Elephas* has usually more than one pyramid in each renculus. The tubi maximi, again, may well be better developed in *Loxodonta*, as they are described as conspicuous structures by DÖNITZ, but are, as it would seem, usually not large in *Elephas*. The material hitherto examined does not allow of definite conclusions, but it seems probable that the kidneys of *Elephas* and *Loxodonta* have developed along slightly different lines.

Sirenia.

Survey of the form of the kidney.

I have only examined a kidney in alcohol of *Trichechus manatus* L. The dimensions are about $160 \times 80 \times 40$ mm. The surface has several shallow grooves. The pelvis has short branches (fig. 16 *C*, p. 343), each with an area cribrosa at its end. The collecting ducts do not open on papillae, but the surfaces of medullary pyramids bordering the pelvis are concave. A few of the collecting ducts are larger than the others, and may perhaps be regarded as small tubi maximi. The medullary parts seem to be completely separated by the cortex. The latter is about 7 mm thick, and the medulla at most about 20 mm. No subdivision into zones is visible in the medulla.

PETIT (1925, p. 23—38) has given an account of the kidney structure in *Manatus latirostris* Harlan (= *Trichechus manatus* L.) and *M. senegalensis* Desm. The surface may have grooves or it may not. The structure of one kidney of each of the two species seems to show great resemblance to the kidney examined by me. As PETIT (1925) points out it is difficult to fit the *Trichechus* kidney into any scheme of kidney types. It seems to represent a transitional stage between kidneys with undivided cortex and divided medulla, and the renculi kidneys. The medullary pyramids do not, however, form papillae. In this respect they resemble those of the elephant kidney, but morphologically this resemblance is of little importance.

The kidney of *Halicore* is well known through the investigations of Freund (1912), Riha (1911) and Petit (1925). Their accounts agree as to matters of structure, but their terminology and opinions differ greatly. The *Halicore* kidney is smooth, and much longer than it is broad. The cortex forms a superficial layer. The medulla is divided into two parts, a cranial and a caudal, each forming a long crest. The pelvis is long with a cranial and a caudal branch, both with numerous processes. As Freund (1912, 1939) points out these branches of the pelvis should not be called recesses, as they have nothing to do with real recesses (= tubi maximi). Freund, on the other hand, calls the processes calices, which is not correct, as they do not lead to, or envelop, papillae.

The *Halicore* kidney cannot well be referred to any of the common kidney types. It is, perhaps, most like the crest kidney, though the crest has been divided into two parts.

Rhytina had renculi kidneys (Steller 1753). Freund (1939, p. 52) doubts this, but gives no sound reasons for his opinion that the *Rhytina* kidney resembled the *Halicore* kidney structurally. In this connection he also writes that in *Manatus* the medulla is originally divided into pyramids, but that later these fuse. It seems that he has interpreted Petit (1925) thus, but I have not been able to find any such statement in the paper by Petit. He also states that the papillary parts of the pyramids fuse in *Halicore*. To my knowledge there is no account of the embryonic development of the *Halicore* kidney, and the anatomical facts do not show such a development.

Artiodactyla.

Hippopotamus amphibius L.

Material. One pair of kidneys in alcohol.

Form. Both kidneys had been cut into two parts previous to fixation, which made the examination difficult.

The dimensions of one of the kidneys is 270 × 165 × 85 mm. The surface is grooved (fig. 17). The pelvis is long and narrow (fig. 17, *pv*). At its end it is joined by two tubi maximi. These pass parallel to the lateral margin of the kidney, at intervals giving off branches (fig. 17, *t.m*). The tubi are narrow (0.5—2 mm). Collecting ducts open in their branches as well as in the tubi maximi proper, though only at certain points. The tubi and their branches are surrounded all along their course by medullary substance, which thus forms a continuous branched mass. The medulla in its turn is covered by the cortex. The whole kidney thus presents a lobated appearance, but the lobes are continuous at their bases. The ends of the lobes, on the other hand, are separated by very

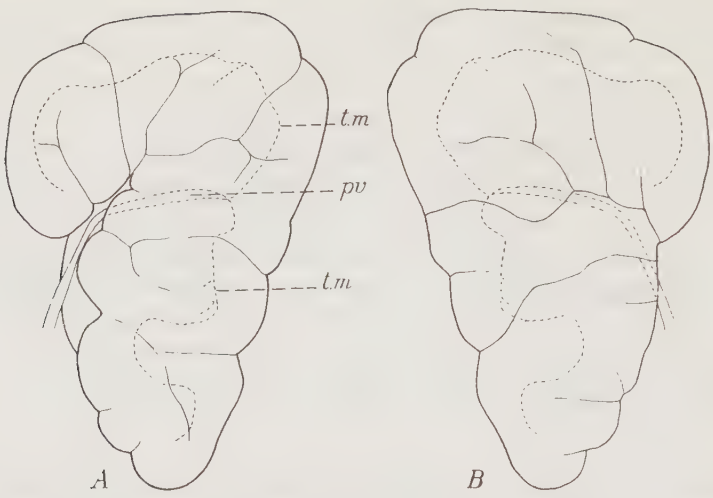


Fig. 17. Kidney of *Hippopotamus amphibius* L. Scheme showing the superficial grooves and the main branches of the tubi maximi. *pv* pelvis, *t. m* tubus maximus. $^1/_4$ ×.

distinct sheaths of connective tissue. The cortex is most often about 12 mm thick, the medulla is about 16 mm thick and shows no division into zones.

The tubules. There are cortical nephrons. Long loops are absent. The proximal tubule narrows continually. The transition into the thin segment occurs at different levels — also in the cortex. The thin segment is at its beginning up to 0.050 mm thick, and though it narrows as it descends it is never less than 0.025 mm thick. The highest cortical nephrons have no thin segments. The loops always turn within the thick segment. The collecting tubules have well-developed arcades, but there are also direct junctions, even in the central parts of the cortex. The central junctions occur already in this region. The collecting tubules are relatively thick in the cortex (0.1 mm).

A cortical nephron and some segments of other nephrons have been measured. It is, of course, not possible to obtain a picture of the average composition of the nephrons from these scanty facts. It is, however, evident that the thin segment constitutes an unusually small part of the nephron; on the other hand the proximal tubules are extremely well developed.

Gerhardt (1911) states that there are 4—5 tubi maximi. His description, however, is very short, and the comparison with *Rhinoceros* and *Elephas* made by him (op. cit. p. 268) only adds to its obscurity. The account of Wehn (1925) is also very difficult to understand, but it seems clear that it is in accordance with my findings. The only exception is that, according to him, the two tubi maximi apparently join

Table 38. *Hippopotamus amphibius, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
hc	240×220	12800×53								12.8
hc	310×285	13800×54								8.4
hc	285×225	14000×51	0	6300×22	3000×40	60	0	27	13	11.1
m	375×340	24000×75								14.1
d	450×320	24300×65								12.2
m	410×300	25000×74								15.0
d	405×310	27800×62								13.7
Mean	320	20242×62								12.5

before opening into the pelvis. It is possible that such is the case in my material, too, but I have not been able to ascertain this. Petit gives a drawing of the form of a *Hippopotamus* kidney (1925, p. 47) which presents the same features as my specimen, and probably the interior structure would, if investigated, have proved similar, too.

Sus scrofa domestica.

Material. Three fresh kidneys.

Form. The kidneys are relatively long. The surface is even. Two of the kidneys belong to young pigs. The weights of these kidneys are 140 gm and 165 gm, and the dimensions are 130 × 54 × 35 mm, and 137 × 60 × 35 mm. The cortex is about 18 mm thick (15—21 mm), the outer zone about 9 mm, and the inner zone 4—7 mm. The third kidney has been obtained from an old sow, and weighs 360 gm; the dimensions are 194 × 85 × 38 mm. The cortex is about 20 mm thick, the outer zone 7.5 mm, and the inner zone about 6.5 mm. The cortex is not divided, but the medulla is divided into several pyramids, each forming a papilla or a crest (fig. 18 *A*). The pelvis is branched.

The tubules. There are many cortical nephrons. The long loops are few and the thin segments are relatively short. In other respects the nephrons show only slight deviations from the common form, and my findings agree qualitatively with the account by Peter (1909). There are relatively few projections on the surface of the distal tubule in the smallest of the kidneys, but in the largest these projections are very numerous and well developed.

The nephrons are difficult to isolate in their entire length. In the smallest kidney proximal tubules 20.7, 23.0, 26.8 and 29 mm long have

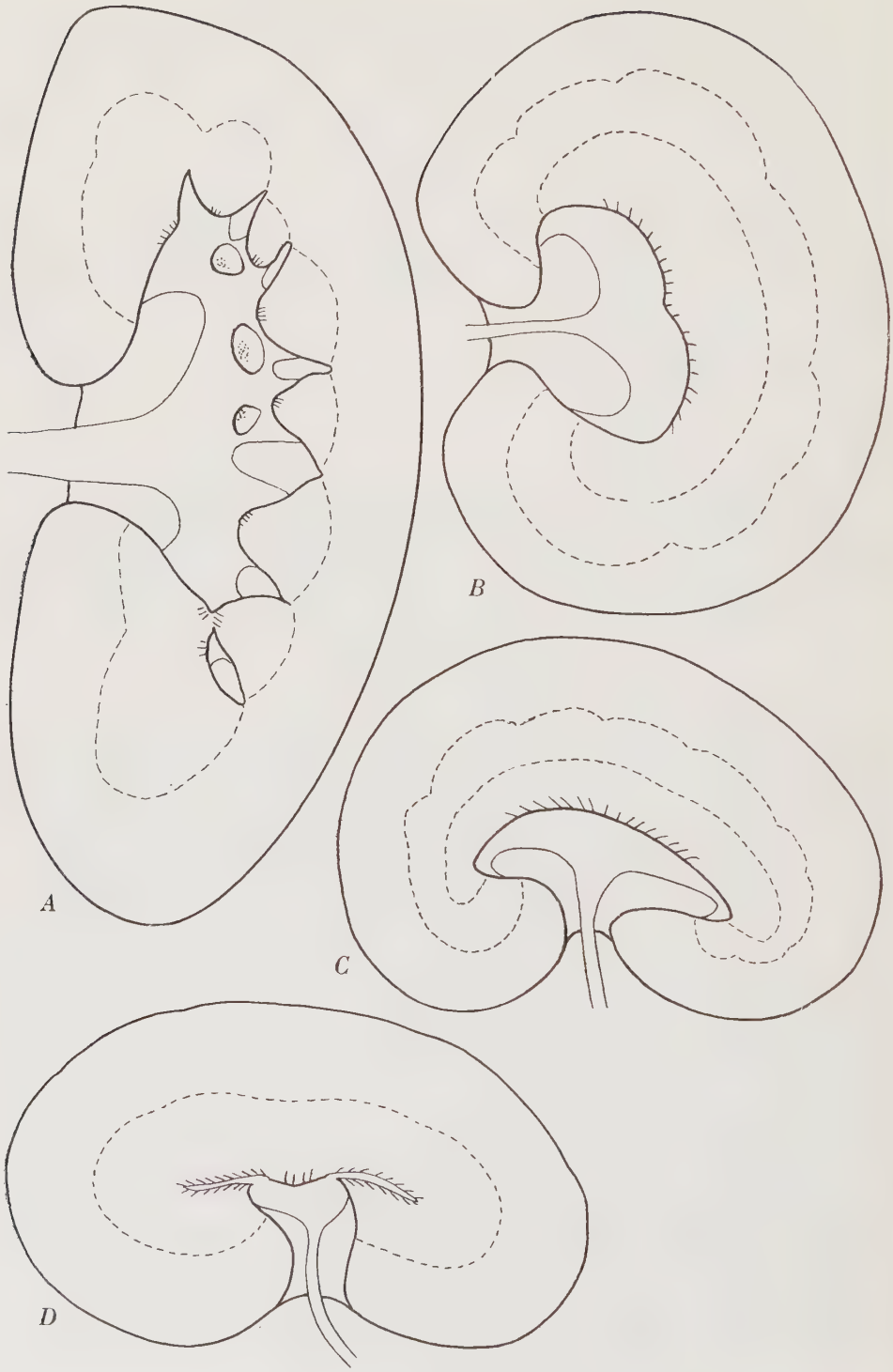


Fig. 18. Kidneys of *A Sus scrofa domestica, B Camelus bactrianus* L. 1/2 ×, *C Alces alces* (L.) 1/2 ×, *D Rangifer tarandus* L.

Table 39 a. *Sus scrofa dom., tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
h	260×190	17000×68	23.4
h	300×230	17300×70	17.6
m	340×260	23300×75	19.8
d	375×300	28500×80	20.3
d	340×240	30000×83	30.5
d	350×300	30000×80	22.9
Mean	290	24350×76	22.4

Table 39 b. *Sus scrofa dom., old female, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
h		29000×59	
h		31000	
h	340×240	33000×60	24.3
d	410×250	36000×66	23.2
d	430×300	36500×70	19.8
m	450×340	37000×68	16.4
d	450×300	38000×62	17.5
m		40800×65	
Mean	351	35163×64	20.2

been measured. In the next smallest kidney the lengths of some proximal tubules measured in addition to those of table 39 a are 22.5, 26.3, 27.8 and 29 mm. The mean length is, then, in this kidney 25 ± 1.3 mm. In the largest kidney an entire cortical nephron has been measured. The dimensions are: Prox. tubule 29 × 0.059 mm, no thin segment, thick segment 6.5 × 0.040 mm, distal tubule 4.5 × 0.045 mm. The lengths of the corresponding segments of a very deep nephron may be assumed to be 38 mm, 20 mm, 10 mm, 7 mm. In this kidney thick segments with lengths 5.5, 6.0, 6.5, 8.5, 8.5, 9.2, 9.8, 10.6, 11.0 and 11.2 mm have been measured. The mean is 8.7 mm. The distal tubule is usually 5—7 mm long, on an average 6 mm. The thin segment is 0—3 mm long in cortical nephrons, on an average 1 mm at most. In short loops it is about 4 mm long (1—6 mm) and in long loops less than 20 mm. If it is assumed that there are some 80 % cortical nephrons and about 3 % long loops, the mean length of the thin segment is about 2 mm. This figure is very uncertain but even large errors in it do not much affect the relative figures for the other segments.

The macroscopic structure of the pig kidney has been examined by many authors. The descriptions usually agree with my findings. Peter's (1909) measurements of the lengths of the tubules are much smaller than mine. His material had shrunk considerably (op. cit. p. 261).

Camelus bactrianus L.

Material. One kidney in alcohol.

Form. There is a typical, long crest (fig. 18 *B*). The pelvis has strongly developed processes. The dimensions are 170 × 130 × 60 mm.

The cortex is about 15 mm thick, the outer zone about 15 mm and the inner zone about 25 mm.

The tubules. The capsule and the proximal tubule resemble those of the cow, but all proximal tubules end at the stripe boundary. The short loops turn within the thick segment, the highest ones about 5 mm above the zone boundary. The thick segment has a thicker and a thinner part. The distal tubule, which begins with a portion with an even contour, has in the following part a very irregular surface, and finally it becomes uniform again. The collecting tubules have well-developed arcades.

Some segments of nephrons have been measured, see table 40. The long loops constitute 55 ± 4.2 % of the total number. The mean length of 11 thick segments is 22 ± 0.9 mm. 5 distal tubules are 3.2—3.7 mm long. A high nephron has been "reconstructed" from parts of two high nephrons. The lengths are: Proximal tubule 33 mm, thin segment 7 mm, thick segment 23 mm, distal tubule 3.7 mm. The available data do not permit an estimation of the proportions of the average nephron. It seems, however, that the thin segment is relatively longer than in the cow, as there are more long loops in *Camelus*. The thick segment is also relatively longer.

Table 40. *Camelus bactrianus, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
d	325×310	26000×57	14.7	*m*	330×240	28500×54	19.4
m	330×285	27000×54	15.5	*m*	270×270	29000×54	21.5
d	315×270	27800×55	18.0	*m*	310×280	29000×55	18.4
m	290×285	28000×60	20.3	*h*	300×290	29300×58	19.5
m	310×280	28000×61	19.7	*m*	300×260	30000×53	20.4
m	300×285	28500×52	17.3	*h*	300×280	33000×53	20.8
d	315×300	28500×51	17.0	*h*	345×285	34500×56	19.6
				Mean	295	29079×55 ±590	18.7

Dama dama (L.).

Material. One pair of kidneys in alcohol.

Form. Dimensions: 80 × 50 × 38 mm. The pelvis is small with slight processes. There is a short crest and the area cribrosa is oval. The cortex is 9 mm thick, the outer zone 11 mm, the inner zone 8 mm.

The tubules. There are a few cortical nephrons. Their loops turn in the central parts of the cortex, and have, normally, a thin segment. There are arcades. The dimensions of some capsules and proximal tubules are given below. The distal tubules have a distinct intercalated segment. Their length is about 3—4 mm, their thickness about 0.037 mm.

	Capsule	Prox. tubule	Ind.
d	285×230	15500×52	12.3
m	280×240	17800×53	14.0
m	300×300	20300×55	12.4
h	260×230	22500×53	19.9
Mean	266	19025×53	14.7

Alces alces (L.).

Material. One pair of fresh kidneys, and one pair in alcohol.

Form. The weight of one of the fresh kidneys is 540 gm. The dimensions are 155 × 105 × 50 mm. The area cribrosa is about 5 cm long, and lies on a low crest (fig. 18 *C*, p. 350). At the extremities two collecting ducts are distinctly larger than the others; they may be regarded as approaches to tubi maximi. The pelvis has slight processes. The cortex is 20—25 mm thick, the outer zone 10—15 mm and the inner zone 10—15 mm. The cortex constitutes about 10 % of the kidney volume.

The tubules. There are cortical nephrons. The proximal tubule is usually thickest in its middle parts. It ends at varying levels, from the stripe boundary to the outer parts of the cortex. The thin segment is absent in the high cortical nephrons, and very short in the low cortical nephrons and the highest nephrons with short loops. The short loops turn within the thick segment. In the high cortical nephrons the thick segment is of uniform thickness, somewhat thicker than the thinner part of the thick segment in the other nephrons.

A nephron with the loop descending to the zone boundary has been "reconstructed" from segments of such nephrons. The lengths of the segments are approximately these: Proximal tubule 26 mm, thin segment 6 mm, thick segment 14 mm, distal tubule 6 mm. The very deepest nephrons ought to have the following segment lengths: Proximal tubule 30 mm, thin segment 35 mm, thick segment 12 mm, distal tubule 8 mm.

Kidneys of an embryo of *Alces* have been examined by Lönnberg (1907). His description is, however, somewhat obscure, and it is difficult

Table 41. *Alces alces, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
hc	200×175	9400×55	15.0	*d*	320×320	26400×75	19.3
hc	240×200	10800×60	13.5	*m*	385×320	27000×75	16.4
hc	240×160	12800		*d*	360×305	27200×75	18.6
h	270×240	16100×72	17.9	*m*	400×275	28000×78	19.9
m	280×280	24000		*d*	335×320	28000×75	19.6
m	330×320	26000×80	19.7	*d*		29500×73	
				Mean	285	22100×72 ±2170	17.8

to understand if there are really separate papillae, as he indicates, or if there are secondary pyramids only. The latter interpretation seems more probable, in view of the structure in the mature specimens examined by me.

Rangifer tarandus L.

Material. One pair of fresh kidneys, one pair in alcohol.

Form. The fresh kidneys weigh about 65 gm each, and the dimensions are 75 × 45 × 27 mm. The cortex is relatively thick, about 15 mm. The medulla is also about 15 mm thick, and not divided into zones visible to the naked eye. The pelvis is small, without processes. There is a small papilla-like crest. At the extremities of the area there are two small tubi maximi (fig. 18 *D*, p. 350). The ratio of the volumes of the cortex and the medulla is about 10: 1 in one of the fresh kidneys.

The tubules. Material from one of the fresh kidneys has been macerated. There is much tough connective tissue, and the tubules are very brittle.

Table 42. *Rangifer tarandus, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
d	165×130	12800×37	22.1	*m*	180×175	15000×42	20.0
	175×175	14300×41	19.1		190×165	17000×44	23.9
h	175×130	14300×42	26.4	*m*	205×165	17300×45	23.0
m	190×175	15000×41	18.5		190×180	17300×44	22.3
h		15000×45		*d*	205×175	18000×43	21.6
				Mean	175	15600×42 ±500	21.9

There are cortical nephrons. The proximal tubules are very looped. In the outer part of the cortex the pars convoluta consists mainly of almost straight segments placed at right angles to the surface of the kidney. These segments are of varying lengths, and are connected by sharp bends. The following nephron segments have not been isolated entire, but they seem to be of normal structure. The long loops are very few, and the inner zone, which is visible microscopically after maceration, is very low. The dimensions of some capsules and proximal tubules are given in table 42. There was a shrinkage of about 20 %.

Ovis aries L.

Material. The kidneys of a young sheep.

Form. One of the kidneys weighs 57 gm, and its dimensions are 71 × 50 × 35 mm. There is a relatively long crest. The pelvis has processes. The cortex is about 7 mm thick, the outer zone 7 mm, of which the outer stripe constitutes 2 mm, and the inner zone 10 mm.

The tubules. The tubules show no marked deviation from the common form, and they also agree in essentials with the description given by Peter (1909). The distal tubules have often small processes (cf. Peter 1909). The dimensions of some capsules and proximal tubules are given below. A high nephron has been isolated: Proximal tubule 21 mm, thin segment 4 mm, thick segment 13 mm, distal tubule 2.3 mm. The very deepest nephrons ought to have about the following dimensions: Proximal tubule 16 mm, thin segment 23 mm, thick segment 8 mm, distal tubule 2 mm. The long loops constitute 36 ± 3.8 % of the total number.

Table 43. *Ovis aries, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.
h		16000×52	
d	240×230	16100×52	15.2
d		16600×53	
m		18000×55	
m	320×240	20000×55	14.3
m	225×225	21000×60	25.1
h	300×240	21900×52	15.8
h	230×220	22000×55	23.9
Mean	247	18950×54	18.9

The sheep kidney has been investigated by several authors (e. g. Toepper 1896, Dumont 1909, Brasch 1909, Agduhr 1917, Marschner 1937). Their descriptions usually agree with my findings. Chiewitz (1897) states that there are tubi maximi. From the account by Müller (1883) it is clear that there may be small recesses at the extremities of the area cribrosa. It is probable that these structures are the tubi maximi of Chiewitz (these recesses seem to be similar to those of the dog and the *Felidae*, cf. p. 333).

As mentioned above Peter (1909) gives a full account of the microscopic structure of the sheep kidney. There is little to add to his description. His material had probably shrunk after maceration, and thus the tubule lengths given by him are probably too low.

Bos taurus L.

Material. Several pairs of kidneys.

Form. The following kidneys have been more thoroughly examined: "Young calf": weight of one kidney 65 gm, dimensions $90 \times 48 \times 21$ mm, cortex 3 mm, outer zone 3 mm, inner zone 8 mm; "Calf": weight of one kidney 290 gm, dimensions $145 \times 90 \times 45$ mm, cortex 4.5 mm, outer zone 8 mm, inner zone 8 mm; "Young cow": weight of one kidney 600 gm, dimensions $210 \times 100 \times 45$ mm, cortex 9 mm, outer zone 9 mm, inner zone 8—10 mm; "Cow": weight of one kidney 500 gm, cortex 9—12.5 mm thick, outer zone 8—10 mm, inner zone 10—12 mm. The surface of the kidney is deeply lobated in the calves (and especially in embryos) and shows distinct, but usually shallow furrows in the old specimens. These furrows correspond to ridges on the inner surface of the cortex. Some of these ridges reach the sinus renis, and divide the kidney into several relatively well-separated lobes (fig. 19 *C*). Most of these lobes are themselves more or less subdivided. On the whole each superficially distinguishable lobe corresponds to a papilla. The superficial grooves in the "Young cow" are shown in fig. 19 *A*, *B*. The main furrows are drawn thicker than the others, though they are not always more distinct on the kidney surface. The upper, well-demarcated lobe *a* contains 3 papillae, two of which resemble crests. The next lobe, *b*, is also distinct and corresponds to 5 papillae, as does the lobe below it. There is one more large lobe, *d*, containing 4 papillae. The small lobe *e* is in close connection with this lobe. There are 3 more small, less distinct lobes in the lower end of this kidney: *g*, *h*, *f*. The pelvis is branched, with a main branch to each of the large lobes, and usually a secondary branch to each distinct papilla. The end part of such a secondary branch may enclose 2—3 papillae. This description refers to the "Young cow".

but the other kidneys examined show a similar structure, though their form varies greatly according to whether they are right or left kidneys.

In the "Cow" the ratio of the volumes of cortex, outer zone and inner zone has been estimated at 81 : 16 : 3.

The tubules. In the "Cow" there are some cortical nephrons, but such have not been found in the other kidneys. In the "Young calf" the proximal tubules end in the whole outer stripe, but in the others they end at the stripe boundary (except, of course, in cortical nephrons).

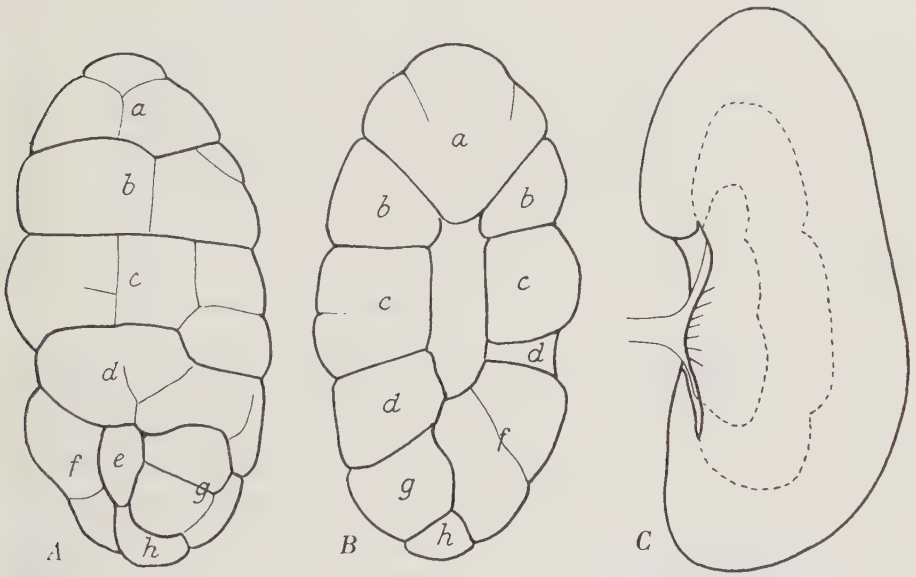


Fig. 19. *A* dorsal, *B* ventral surface of cow kidney. *a*—*h* designate the main lobes. 1/4 ×. *C* section through lobe.

The proximal tubules show a uniform calibre, except in the "Calf", where the terminal part is distinctly thinner and more transparent, with visible cell boundaries. The short loops turn in the central part of the outer zone. In the "Young calf" the macroscopic zone boundary is the region where most short loops turn, but the transition between thin and thick segment in long loops occurs about 1.5 mm below this region. This transition is relatively indistinct, and the long loops are not very numerous; thus the real zone boundary is only distinguishable after microscopic examination. The short loops turn at the transition between thin and thick segment. The thick segment is, in mature specimens, distinctly differentiated into a thicker and a thinner part, but in the "Young calf" no such differentiation is visible, and in the "Calf", too, it is indistinct. The distal tubules are generally divided into three seg-

Table 44 a. *Young calf, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	105×105	4800×29	1300 × 8	4000×14	1200×21	42	12	35	11	12.6
h	125×110	5100×30	1750 × 7	4300×15	1280×22	41	14	35	10	11.1
h	105×105	5200×30	1650 × 8	4300×15	1350×23	42	13	34	11	14.1
h	115×115	5300×29	1500 × 8	4300×15	1100×23	43	12	35	9	11.6
h	120×110	5600×29	1800 × 8	4400×14	1200×24	43	14	34	9	12.3
m	115×105	5700×30	1900 × 9	4700×16	1150×22	42	14	35	9	14.2
m	115×100	5700×31	2200 × 8	4800×15	1050×23	41	16	35	8	15.4
m	120×105	5800×30	2000 × 8	4700×16	1200×22	42	15	34	9	13.8
dd	130×100	5900×29	(12000)× 9	4800×16	1000×22	(25)	(50)	20)	(5)	13.2
d	145×110	6300×33	5600 ×10	4900×16	900×23	36	32	28	5	13.0
Mean	113	5540×30 ±75	2188 × 8	4520×15 ±94	1143×23					13.1

Table 44 b. *Calf, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
d	180×165	14300×47	14	9800×23	3400×40					22.6
h	195×175	17000×45	3800×12	11000×25	3000×40	49	11	32	9	22.4
h	190×170	17200×45								24.0
h	195×190	18000×43		11000×23	3500×41					20.9

Table 44 c. *Cow, tubule dimensions in μ.*

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
h	275×250	17100×45	11.2	*h*	375×335	26000×64	13.2
d	270×260	20000×50	14.2	*h*	375×300	30800×60	16.4
d	295×250	20300×53	14.6	*h*	300×280	32000×68	25.9
m	295×240	22500×58	18.4	*h*	325×280	33800×62	23.0
m	330×265	23500×61	16.4	*h*	335×315	34000×70	22.6
h	375×375	25000×62	11.0	*h*	370×290	35000×70	22.8
m	325×255	25500×68	20.1	Mean	305	26576×61 ±1650	17.7

ments (cf. Inouye 1909). The collecting tubules have well-developed arcades.

The dimensions of some nephrons are given in tables 44 a, b, c. In the "Young calf" there was a shrinkage of about 10 %. The mean of the table may be accepted as representing the average nephron. In the "Calf" the long loops constitute 20.8 ± 2.4 % of all loops. Proximal tubules 15.8, 16.5, 16.8, 17.0, 17.3 and 18.2 mm long have been measured in addition to those of the table, and also thick segments 10.0, 10.2, 10.5, 10.7, 10.8, 10.8 and 11.1 mm long. The corresponding means are 16.8 and 10.6 mm. In the "Young cow" there is a shrinkage of about 10 %. The proximal tubule measures 17.8 ± 0.4 mm (17 data) and the thick segment 11.5 ± 0.2 mm (15 data). The long loops constitute 21 ± 2.8 % of the total number (Inouye's countings give 24 ± 1.2 %).

In the "Cow" the segments in a high nephron are 35, 5, 16, 7 mm long resp. The proximal tubule is about 27 ± 1.6 mm long, the thick segment is, on an average, 15 ± 0.5 mm, and the distal tubule about 5 mm. The thin segment is about 5 mm long in short loops. The mean length of long thin segments may be estimated at 10—15 mm, probably about 12 mm, the mean of all thin segments at 7 mm. The proximal tubule would thus constitute about 50 % of the average nephron, the thin segment 13 %, the thick segment 28 %, the distal tubule 9 %.

The form and structure of the cow kidney have been described by several authors. Their accounts most often agree with my findings. Ellenberger and Baum (1926), and also Marschner (1937), and Freund (1939), state that the lobes merge in the outer zone. This is not true. All papillae are separate up to the cortex. The lobes are connected by the cortex and the blood-vessels, the pelvis, and the connective tissue.

Artiodactyla, survey of the form of the kidney.

Neobunodontia. In *Sus* there are several papillae. In *Phacochoerus* there is either a crest as Petit (1925, p. 131) states (also my own examination of an embryo), or there are some papillae (Gerhardt 1911, Lönnberg 1912). I have re-examined Lönnberg's specimen (fig. 20 *A*); it is akin to the crest kidney. Hyrtl (1872) states that the renal pelvis of *Dicotyles* is similar to that of *Sus*. Chiewitz (1897), on the other hand, found a crest with two tubi maximi. This agrees with the structure in a young specimen examined by me (fig. 20 *B*). The processes of the pelvis are very faint in my specimen.

It seems that the kidney structure varies greatly in *Suidae*. It is most probable that the crest kidney is the most primitive condition, and from this the kidney with papillae and the kidney with tubi maximi have developed. If this is so the kidneys with papillae in *Sus* and in

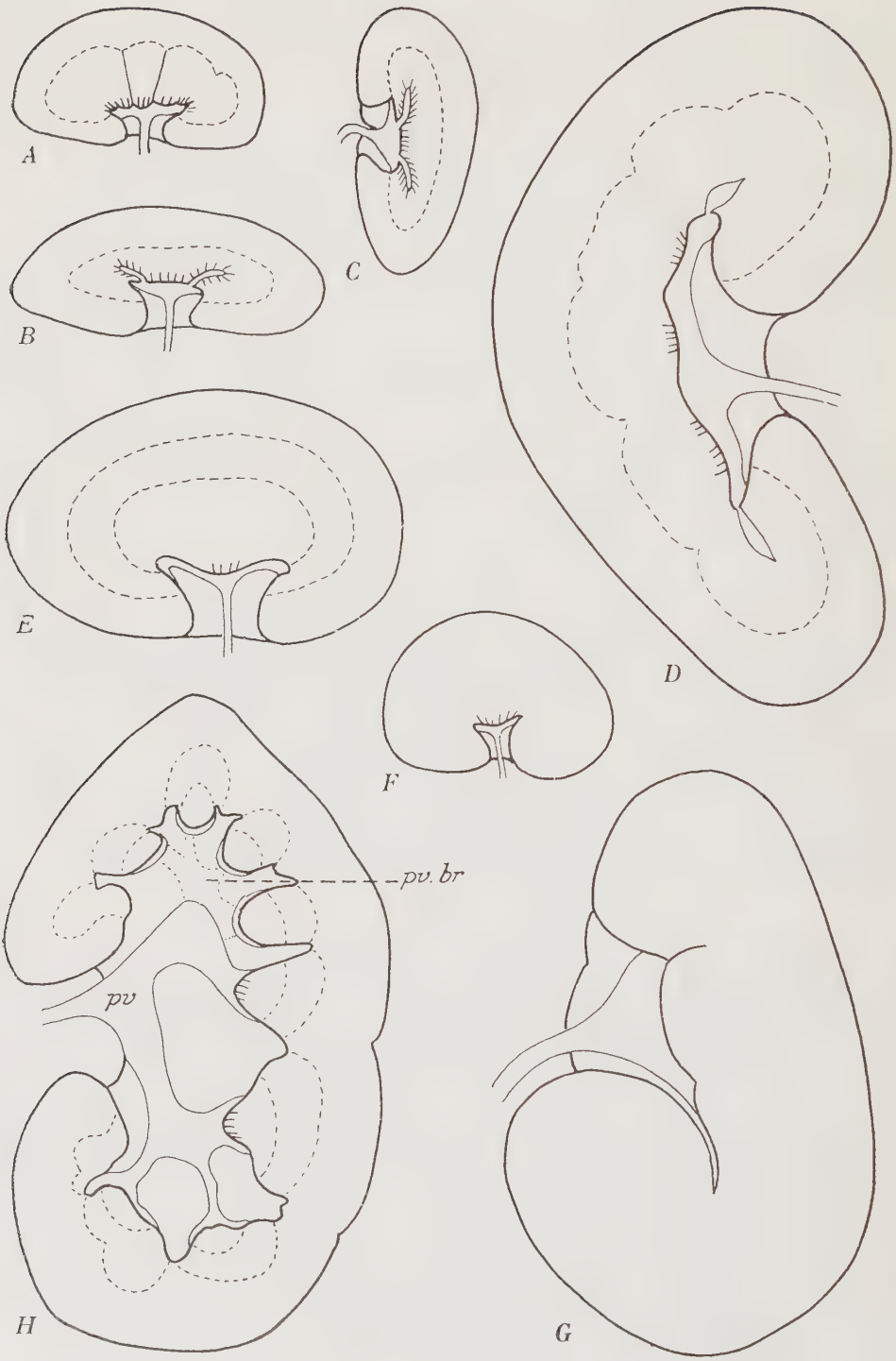


Fig. 20. Kidneys of *A Phacochoerus sp., B Dicotyles tajacu* L., *C Tragulus javanicus* Osb., *D Cervus elaphus* L., *E Antilope cervicapra* L., *F Cephalophus melanorhoeus* Gray, *G, H Anoa depressicornis* H. Sm. *pv.br* pelvic branch.

Phacochoerus must be considered to have developed independently of one another.

In *Hippopotamus* there are branched tubi maximi, which condition is unique among the mammals hitherto examined.

Ruminantia. *Camelus* and *Lama* both have typical crest kidneys (Hyrtl 1872, 1873, Gerhardt 1899, Lesbre 1903, p. 106, Freund 1939). In *Camelus* the crest is long.

Tragulus javanicus Osb. has oblong kidneys. Two tubi maximi open at the extremities of the area cribrosa, which lies on a short crest (fig. 20 *C*). The medulla is not divided into zones, and there are no pelvic processes.

Hyrtl (1872) has examined the form of the pelvis in *Capreolus, Cervus barberinus* and *Cervus pseudoaxis* (= *Sika* Sclater). There is a crest, and the pelvis has processes. Similar statements are given by Chiewitz (1897) on *Dama dama* (L.), and *Odocoileus virginianus* Bodd. Petit (1925, p. 126) describes the kidneys of *Rucervus eldi* Guthrie and *Rusa unicolor* Bechst. He states that, in the latter, there is a long crest. He calls the cranial and the caudal end of the pelvis recessus terminales (= tubi maximi). From the description it seems that there are no true tubi maximi. I have myself made dissections of the kidneys of *Dama* and *Cervus elaphus* L. only. In the latter there is a long crest, and the area cribrosa is divided into some groups of pores. In one of the specimens examined there are two wide, flattened tubi maximi (fig. 20 *D*); in the other the tubi maximi are very narrow.

It seems that the kidney structure in other *Cervidae* also may be more complicated than most of the statements in the literature imply.

Hyrtl (1872) states that the *Capreolus* kidney he examined showed superficial lobation. Freund (1939) is convinced that this statement must be due to some error, as he has not found any lobated kidneys among several examined by him. In this connection it may be mentioned that Wiedersheim (1909, p. 701) figures a *Capreolus* kidney with marked lobation. It seems possible that there may be individual variations in this respect.

Rangifer has a short crest with small tubi maximi (p. 354). In *Alces* there is a long crest with only traces of tubi maximi.

All antelopes hitherto examined have simple kidneys. Most often there is a crest, but in *Antilope cervicapra* L. there is a low papilla (fig. 20 *E*). The following have been examined by Lönnberg (1901, 1903, 1912), and Petit (1925): *Connochaetes gnu* Zimm., *Connochaetes taurinus* Burch., *Cephalophus ogilbyi* (Waterh.), *C. melanorhoeus* Gray (cf. also fig. 20 *F*), *C. harveyi keniae* Lönnb., *C. dorsalis* Gray, *Nesotragus moschatus* v. Dueben, *Rhynchotragus guentheri wroughtoni* Drake-Brockman, *Cobus*

ellipsiprymnus (Ogilby), *Antidorcas euchore* Sparm., *Antilope cervicapra* L., *Gazella dorcas* L., *Taurotragus livingstoni* (Sclater), and *Gazella rufina* Thomas. *Taurotragus livingstoni* (Sclater) has been investigated by Agduhr (1917), and the pelvis of *Antidorcas euchore* Sparm. by Hyrtl (1872). The descriptions are, however, usually so short and incomplete that it is difficult to obtain a clear picture of the structure of the kidneys described. This is still more the case in some reports of Murie (e. g. 1870). Hyrtl (1872) states that the renal pelvis of *Antilope pygmaea* is branched. I doubt this, as does Freund (1939). In a specimen of *Antilope euchore* Hyrtl thought that he had found a small papilla, separated from the main papilla, and enclosed by the pelvis in a similar way to a normal papilla. Freund (1939) cites this. This is obviously erroneous. The part of the medulla taken by Hyrtl for a papilla is only partly separated from the rest of the medulla (cf. Hyrtl 1872, Pl. III, fig. 5). The processes of the pelvis surround it circularly; a papilla is surrounded by a cup-shaped calix.

All sheep and goats examined have kidneys with a crest, and the pelvis has distinct processes.

Ovibos moschatus Zimm. has a typical crest (Lönnberg 1900).

Among the *Bovinae*, *Anoa* has a grooved surface to the kidney, and there are several papillae (Lönnberg 1903). The grooves are shallow, and the cortex projects slightly between the papillae (fig. 20 *H*). The pelvis is branched. In the cow the grooves are deeper and the kidney is divided into lobes, but these are not so well separated and independent as in a typical renculi kidney. According to Lönnberg (1912) and Petit (1924 a) the kidney of *Bubalus* is a more typical renculi kidney. The kidney of a calf of *Bison bonasus* (L.) is similar to that of a cow. *Bison bison* (L.) has a branched renal pelvis (Hyrtl 1872). The kidney of *Poëphagus* is similar to that of *Bos* (Lönnberg 1907).

The kidney of *Giraffa* has a long crest (Hyrtl 1873, Gerhardt 1899).

From the facts hitherto known it seems most probable that the crest kidney, or some similar type, is most primitive in *Ruminantia*. From this have developed types with tubi maximi and types with lobes. The former condition is known from *Tragulus* and the *Cervidae*. In these two groups tubi maximi must have developed independently. It is not possible to say with certainty if this type has been developed more than once in *Cervidae* also. The development towards the renculi kidney can be traced in *Bovinae*.

Kidneys with papilla occur only among the antelopes (*Antilope cervicapra*). It is, of course, possible that these are the most primitive (cf. p. 400), but if the order is studied without regard to other orders there is little reason to think so.

The medulla is divided into zones in *Camelus, Dama, Alces, Antilope cervicapra, Taurotragus, Connochaetes, Ovis, Capra, Anoa, Bos.* The inner zone is absent in *Tragulus*, and is very faint in *Rangifer* and probably in *Cephalophus melanorhoeus.* It seems most likely that the primitive condition is the occurrence of distinct zones, and the reduction of the inner zone has taken place independently in several types.

The occurrence of pelvic processes varies, but the material is too small to allow of any conclusions as to which condition may be the primitive one.

Perissodactyla.

Equus caballus L.

Material. One pair of fresh kidneys, one kidney in alcohol.

Form. The total weight of the fresh kidneys is 1570 gm. The dimensions are 185 × 130 × 60 mm, and 165 × 165 × 60 mm. The corticomedullary boundary is somewhat indistinct, owing to the numerous thick medullary rays. The cortex is about 14 mm thick, the outer zone about 16 mm, of which a distinct outer stripe occupies 5—6 mm, the inner zone up to 21 mm. The pelvis is small with slight processes. The area cribrosa lies on a small crest, at the extremities of which open two long and large tubi maximi (fig. 21).

The tubules. The capsule is transversely oval or round. There is sometimes a very short neck. The proximal tubule first widens and then remains of uniform thickness for a considerable length. The last part of the convoluted portion becomes more narrow and transparent; this appearance is retained throughout the pars recta. The highest proximal

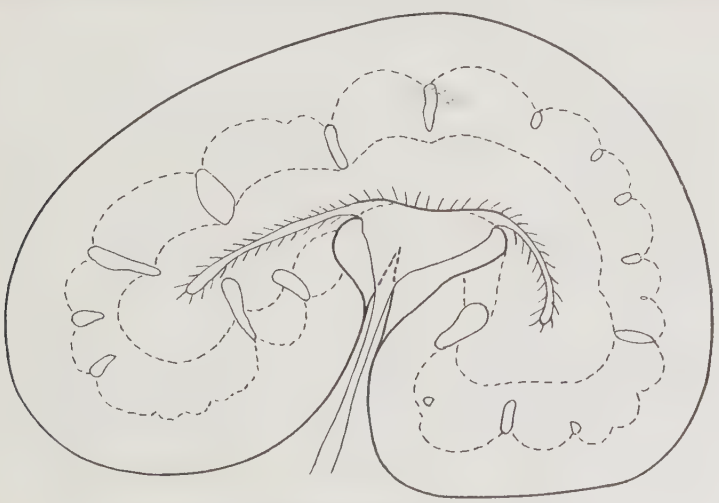


Fig. 21. *Equus caballus* L., kidney. $^1/_2$ ×.

tubules end at the cortico-medullary boundary. In some of these the thin segment may be absent. Thus, though strictly speaking there are no cortical nephrons, there are nephrons quite comparable to such. The short loops turn within the thick segment, which is always differentiated into a thicker and a thinner part. The distal tubule begins with an intercalated segment, which resembles the thinner part of the thick segment. Then the true distal tubule follows. This is thick and opaque. It narrows towards the end. In some nephrons there is a segment between the distal tubule and the collecting tubule, resembling the latter. It is not, however, transparent, as initial collecting tubules normally are, but may, of course, deserve this name notwithstanding. The distal tubules most often open directly into the collecting tubules. The latter have arcades, and their first central junctions usually occur in the outer zone. The arcades often collect about 10 nephrons, but a few arcades turn already in the inner part of the cortex, and then collect only a small number of nephrons. The collecting tubules are relatively thick, also in the cortex (up to 0.12 mm). In addition to these thick collecting tubules, there is in the medulla much connective tissue. Thus, the thin segments constitute a relatively small part of the volume of the medulla.

The dimensions of some nephrons and segments are given below. There was a shrinkage of about 10 %. 13 long and 54 short loops have been counted, together with 2 loops without thin segment.

Table 45. *Equus caballus, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	270×250	28000×59	5000×18	17000×26	2500×45	53	10	32	5	24.5
m	335×230	25000×60	5800×20	16600×28	2200×40	50	12	33	4	19.5
dd		(22000)	(40000)	(14000)	(3000)	(28)	(51)	(18)	(4)	

	Capsule	Prox. tubule	Ind.		Capsule	Prox. tubule	Ind.
d	330×265	21000×64	15.4	*m*	300×240	23500×65	21.2
m	300×235	21400×61	18.5	*h*	280×250	24500×60	21.0
d	315×240	21500×60	17.1	*m*	375×225	25500×63	19.0
m	280×230	21800×59	20.0	*h*	370×220	27000×56	18.6
m	250×240	23300×58	22.5	Mean	274	23863×60 ±710	19.8

The mean length of the thick segment is about 15 mm (12 measurements), and that of the distal tubule 2.9 mm (15 measurements). These segments are on an average 0.027 and 0.042 mm thick. The thin segment is about 3.5 mm long in short loops. The average length of the thin segment in long loops is probably not over 20 mm. The mean length of this segment may thus be estimated at about 7 mm. The values for the segments of the nephron have been corrected for the shrinkage. If this is done with the mean length of the proximal tubule, too, it becomes about 26 mm. The average nephron may thus be assumed to have the following composition: Proximal tubule 51 %, thin segment 14 %, thick segment 29 %, distal tubule 6 %.

The structure of the horse kidney has been investigated by several authors (cf. esp. Skoda 1914). Toepper (1896) states that the tubi may be absent, but this is not accepted by most later writers. Siewert (1927) has examined the form of the tubules. Most of his statements hold for the specimen examined by me. He found, however, a long neck and, also, typical cortical nephrons.

Perissodactyla, survey of the form of the kidney.

The horse and the zebra have kidneys with tubi maximi (Hyrtl 1872). The kidney of the tapir also has tubi maximi (Hyrtl 1872, Gerhardt 1911, Petit 1925).

Gerhardt (1911) states that there are 4—5 long tubi maximi in *Rhinoceros*, and compares the structure with that of *Hippopotamus* and *Elephas*. This comparison makes his statement dubious, as the elephant kidney is a renculi kidney, and the *Hippopotamus* kidney probably has only two tubi maximi (cf. p. 347). The figure of a *Rhinoceros* pelvis given by Hyrtl (1872, Pl. II, fig. 3) shows a condition very similar to that of the elephant, with a branched pelvis, the ends of which seem to have enclosed low papillae. Thus it would seem most probable that the *Rhinoceros* kidney is also composed of renculi. This conception is supported by my finding the kidneys of a *Diceros bicornis* embryo to be strongly lobated. They appear to be typical renculi kidneys, but their inner structure is not so differentiated as to allow of any definite conclusion.

It thus seems that there are in the *Perissodactyla* two types of kidneys, neither of which can be assumed to have developed from the other. There is also no clue as to what common type they may have developed from.

Primates.

Chiromys madagascariensis (Gmelin).

Material. One pair of kidneys in alcohol.

Form. The dimensions of one kidney are $20 \times 12 \times 9$ mm. The cortex is about 2.5 mm thick, the outer zone 3 mm, the inner zone nearly 5 mm. The papilla is long and pointed (fig. 22 *A*).

The tubules. The capsules are usually round. The proximal tubules are thickest at the beginning, and their distal part is more slender (normally about 0.030 mm thick). The short loops turn near the zone boundary. They often turn within the thin segment. This makes it difficult to distinguish between short and long loops. The thick segment is slenderer in the outer zone than in the cortex — the reverse of the normal condition. The distal tubules frequently have a short intercalated segment, which is often slightly thinner than the last part of the thick segment. The transition into the initial collecting tubule is very indistinct; thus, it is very difficult to determine where the distal tubule ends. There are a few small arcades.

The dimensions of some nephrons are given below. 8 long and 25 short loops have been counted. The average length of the thick segment is 3.4 ± 0.1 mm (11 data). The mean length of the proximal tubule is 5.11 ± 0.22 mm including the following data: 4.5×0.038, 4.7×0.040, 4.8, 5.1, 5.3 mm. The mean length of the distal tubule is 1.53 mm.

Table 46. *Chiromys madagascariensis, tubule dimensions in μ.*

	Capsule	Prox. tubule	Thin segment	Thick segment	Dist. tubule	Segment length %				Ind.
						p. t.	t. s.	th. s.	d. t.	
h	130×105	4400×40	1100×8	3800×29	1100×36	42	11	37	11	12.9
h	140×115	5100×42	1400×8	3800×28	1600×34	43	12	32	13	13.3
d	140×140	5200×43		2900×28	1400×35					11.4
m	140×115	5300×41	1400×8	3500×26	1600×38	45	12	30	14	13.5
dd	150×140	6700×40	(11000)	(2800)	(2000)	(30)	(49)	(12)	(9)	12.8
Mean	132	41	8	28	36					12.8

Primates, survey of the form of the kidney.

The macroscopical structure of the primate kidney has relatively recently been the subject of an investigation by Straus (1934). Straus makes a critical and almost complete examination of the relevant literature.

Thus, there is no need here to give more than a summary of his paper, and a few additional notes.

In *Lemuroidea* there is a papilla (cf. figs. 22 *A*—*C*). In a kidney of a *Galago sp.* I have, however, found a transitional type to the crest type (fig. 22 *D*).

In *Tarsioidea* there is a papilla (cf. fig. 22 *E*).

Among the New-World monkeys *Ateles* may have a crest or two papillae, but usually there is a papilla in the other forms.

Among the Old-World monkeys there are forms with papilla and

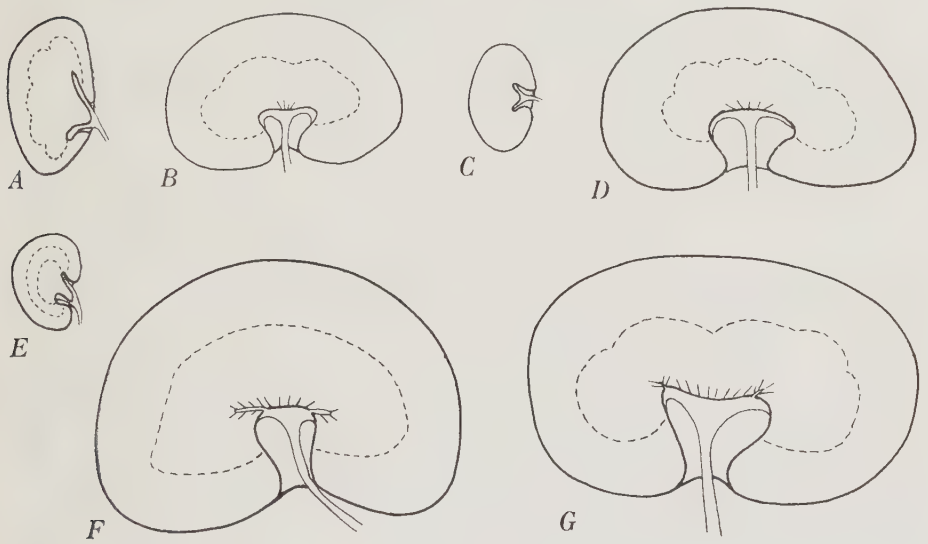


Fig. 22. Kidneys of *A Chiromys madagascariensis* (Gmelin), *B Lemur catta* L., *C Galago sp.*, *D Galago sp.*, *E Tarsius tarsius* Erxl., *F Macacus sylvanus* L., *G Papio sp.*

with crest. In *Macacus sylvanus* L. there are, however, distinct but small tubi maximi, and similar but still less developed structures exist in a *Papio sp.* (fig. 22 *F* and *G*). There are a number of statements that the anthropoid apes possess several papillae. Like Straus I am convinced that the majority of these statements refer to subdivisions of a single papilla. Straus is of the opinion that the description of two papillae in an Orang-utan by Mijsberg (1923) must be accepted. Straus seems to have overlooked the figure of a branched *Hylobates* pelvis given by Hyrtl (1873, Pl. X, fig. 4). This pelvis must have belonged to a kidney with 6 papillae. Straus does not mention the paper by Gerhardt (1906), where the latter states that the kidneys of a Gorilla female had 5 and 6 papillae. It seems, however, that these kidneys are the same as those figured by Gerhardt in 1914 (Pl. III), as the measurements are identical

and the source probably the same. From these figures it is clear that there is a crest in each kidney. Later Koch (1937) has given a short description of the kidneys in a Gorilla male. He says there are 4 papillae (op. cit. p. 6). Westenhöfer (1937, p. 30) says, however, with reference to the same kidney, that there are 3 groups, each with two medullary pyramids. From the photograph given by Koch (1937) it seems clear, however, that there must be a division of the medulla into true papillae. The cortex is thick, and shows no traces of division. Thus it seems that the kidneys of Orang-utan and Gibbon are normally simple, but sometimes show more than one pyramid. So little material from Gorillas has been examined that it is impossible to know what the normal condition is. In the Chimpanzee only simple kidneys are known (cf. also Rumpf 1937, who figures a crest kidney of this form). I myself have examined one kidney from Orang-utan and from Gibbon, and 4 pairs from Chimpanzee, all simple.

In Man only kidneys with more than one papilla are known. The number of papillae varies greatly, however. Though the surface is normally smooth, the human kidney is structurally a lobated kidney, rather closely resembling the typical renculi kidney. The closest resemblance seems to be with the cow kidney.

From the hitherto examined material it seems hardly possible to draw any other conclusion than that the simple kidney with a papilla is the primitive type in the *Primates*. From this the form with a crest must have developed; the kidney with papillae in *Ateles* and the anthropoid apes, and the kidney with tubi maximi in *Macacus* and *Papio* have probably originated from that type. It also seems probable that the human kidney type has developed from the crest kidney, probably via some transitional stage similar to that of *Ateles*. Bolk (1921), Mijsberg (1923) and Wood Jones (1929) consider the human kidney the most primitive among the *Primates*. From the viewpoint of comparative anatomy there seems to be nothing to support this opinion, at least as far as the *Primates* are concerned. Straus is of opinion that "the phylogenetic history of the kidney is by no means clear". It is probable that the position of the human kidney can be correctly estimated only after a wider survey (cf. p. 400).

The medulla is divided into zones in *Lemur catta*, *Chiromys*, *Tarsius* and *Homo*, but in *Lemur* the inner zone is very low and there are some cortical nephrons, as in Man. In *Macacus sylvanus* and *Papio sp.* there is no inner zone, but many cortical nephrons.

III. General section.

Observations on the structure of the tubules.

The nephron segments and the collecting tubules.

The nephron segments. The capsule of Bowman is of uniform structure. The epithelium is sometimes thicker in some parts of the capsule, but this feature seems very variable and has probably no morphologic significance (cf. Mac Nider 1927). The shape also varies, but there seems to be no regularity in the distribution of the forms.

The neck is individual in its occurrence, too.

The proximal tubule often shows slightly differentiated parts with regard to diameter, transparency and granule content. Some of these differentiations seem to be individual variations, but one is certainly of greater significance: a distinct terminal segment in some *Carnivora*. This is well known in the cat and the dog (cf. p. 320 and 325), where the terminal segment is usually very distinct. A similar, thickened terminal segment exists in *Ursus* (p. 327), *Lutreola* (p. 330), sometimes in *Mustela* (p. 329) and in *Phoca hispida* (p. 336). It is thus a wide-spread feature in the *Carnivora*, though it is absent in *Arctitis*, *Lutra* and sometimes in *Mustela*. It must be assumed that there is also a terminal segment differentiated in those carnivores where it is apparently lacking. In these forms it is probable that its existence cannot be ascertained owing to the uniform diameter of the proximal tubule.

In several forms belonging to other groups there is a terminal segment which is most often narrower than the preceding part of the proximal tubule. It is usually more transparent than the latter (shrews, Pl. 3, fig. *1*; rabbit, *Sciurus*, *Mus*, Pl. 2, fig. *3*; sometimes in the cow, horse), but in *Pipistrellus* it is more opaque. The transition seems to be gradual in these forms. In the white rat (Pl. 1, fig. *5*) and in *Hystrix* (Pl. 2, fig. *1*) the transition is abrupt, and the terminal segment is thicker than the preceding part of the proximal tubule. In all these forms it is possible to see cell boundaries in the terminal segment, but not in the other parts of the proximal tubule. In many mammals there is thus a terminal segment which is anatomically distinguishable and probably comparable with that of the carnivores. It is reasonable to suppose that, in the

other mammals also, there is a similar differentiation of the proximal tubule, though it is indistinguishable in the maceration preparations used by me.

Suzuki (1912) has divided the proximal tubule into 3—4 parts on the basis of their structure. Of these parts the distal one is probably the same as the terminal segment. The segments distinguished by him in the proximal part of the proximal tubule seem somewhat doubtful. His investigations refer to guinea-pig, mouse, rabbit and hedgehog.

The thick segment is as a rule differentiated into a thicker and a thinner part. Sometimes it is uniform. This is especially the case in cortical nephrons, but it may also be so in all nephrons of a kidney (*Jaculus*, young calf, young rabbit, young cat).

The distal tubule is often composed of distinct segments. The first of these, the intercalated segment (Pl. 3, fig. *2*, *3*), is often structurally identical with the thinner part of the thick segment. In this case it would perhaps be appropriate to refer the intercalated segment to the thick segment, and not to the distal tubule. From a practical point of view it is, however, better to refer it to the distal tubule, as the beginning of the latter is usually most accurately determinable if the point of attachment to the capsule is taken as the boundary between thick segment and distal tubule. The other distinct segments of the distal tubule (cf. esp. *Erinaceus* and cow) vary so greatly in occurrence and appearance that it is not possible to give any general scheme.

The distal tubule is usually not provided with numerous projections. Especially in the small forms and in young specimens there are very seldom as many projections as Peter has found in several larger forms.

The collecting tubules. As described in the introduction there are two main types of collecting tubules, the collecting tubule with direct junctions, and the arcade. These types have been described by several writers, especially by Peter (1909), who has reviewed the earlier literature. After him only v. Möllendorff (1930, p. 15—18) seems to have treated this subject. He considers the arcades to be more primitive.

To answer the question as to the nature of the arcades, it is necessary to find out their essential characters. The most important are that their first, ascending part does not lie in the medullary ray, as does the descending part, and the fact that the deepest nephrons open in the very beginning of the arcade. That the ascending part of the arcade has the situation mentioned is pointed out by Peter (1909) and v. Möllendorff (1930), and after thorough examination of a number of kidneys of rabbit and cow I can confirm this. Occasionally this matter has been examined in other species also, without any exception appearing. This is important, as the collecting tubules with direct junctions lie entirely in the medullary

rays when they pass through the cortex. The order of junction by the nephrons indicates more directly which type is primitive, however. In the hitherto examined *Amphibia*, reptiles and birds, the nephrons open into the collecting tubule in the order in which they were formed, the oldest nephrons opening nearest to the base of the collecting tubule (see especially Huber 1917, also Zarnik 1910). This must be considered the original mode. This same order also normally occurs in the collecting tubules with direct junctions in the mammals. In the arcades this order is reversed. This must be considered secondary. In most land vertebrates the kidneys are composed of lobuli (Zarnik 1910, Huber 1917, v. Möllendorff 1930). In these the collecting tubules are situated at or near the surface of the lobuli, together with the afferent veins; the artery and the efferent vein of the lobulus are separate from these two and often lie in the centre of the lobulus. The part of the lobulus containing the collecting tubules corresponds to the medullary rays in mammals (cf. v. Möllendorff 1930, Freudenberg 1931). The artery and vein are situated separate from these; v. Möllendorff considers them as the centre of mammalian renal lobuli. (Traut 1923 and Huber 1928 take another view of the lobular composition in the mammalian kidney, but it does not affect the following argument even if their view is accepted). The position in the medullary rays must then be considered primitive for the mammalian collecting tubule. It seems reasonable to think that the ascending part of the arcades, to which nothing seems to correspond in other vertebrates, has either been secondarily formed, or has changed its place secondarily.

The mammalian collecting tubules deviate from the reptilian type in one further respect. In the latter the initial collecting tubules open into the collecting tubules, and not only into their end branches, but also into the more basal parts (fig. 23 *A*, cf. Zarnik 1910 and Huber 1917). In the mammals the initial collecting tubules normally join only the end branches of the collecting tubules, and there is usually a long portion of them receiving no nephrons (fig. 23 *B*). The mammalian type is certainly secondary, and may be supposed to have developed either through the complete reduction of the deepest nephrons in the reptilian type, or through the displacement of their junctions towards the end of the collecting tubules (instead of this last possibility a cleavage of the collecting tubules might be supposed, so that the branchings have moved downwards). Fig. 23 *C* is a schematic representation of a collecting tubule in a bird (after Huber 1917). If a moderate displacement of the deepest junctions occurs, a typical mammalian collecting tubule without arcade results (fig. 23 *D*). If the displacement is much greater in the deepest nephron than in the next deepest, the former may come to open into

the collecting tubule above the latter. Such types of collecting tubules are sometimes found (fig. 9: *2*, p. 307). If there is some displacement in the higher nephrons, but none in the deepest, a type will result similar to that shown in fig. 11: *5*, p. 319). It is also possible to assume that the deepest nephron may be displaced in such a way that it joins the initial collecting tubule above it instead of the collecting tubule. The resulting type (fig. 23 *E*, cf. fig. 11: *8—11*) has a small arcade. If such a process is taken one step further (fig. 23 *F*, cf. figs 9: *2*, *4*; 11: *13*; 13 *C*, p. 325) a more typical arcade is formed. As the distal tubules and the initial

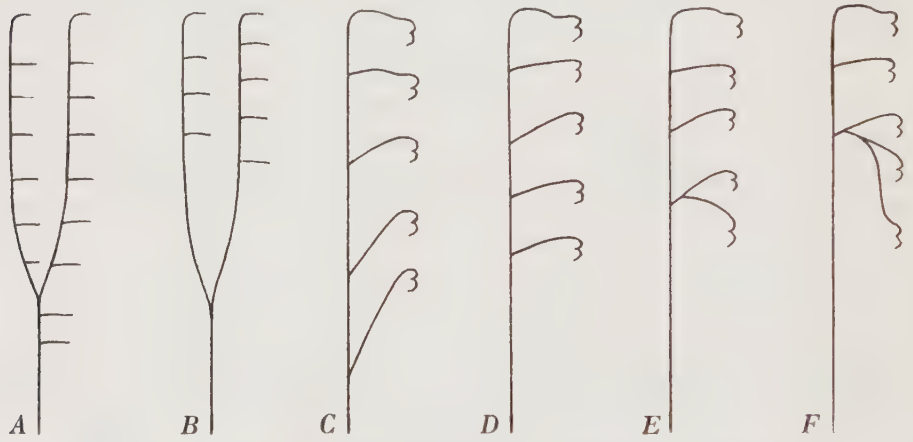


Fig. 23. Schemes of collecting tubules. Explanation in the text.

collecting tubules lie between the artery and the medullary ray the new portion of the collecting tubule thus formed will not lie in the medullary ray, but in the neighbourhood of the artery. This assumed process is thus capable of explaining the three main characteristics of the mammalian collecting tubules: The junction-free segment, the situation of the arcade, and the reversal of the order of junctions in the arcade. The small aberrations described above may be attributed to small irregularities in the process. Another relatively common type is that shown in figs. 9: *3*, p. 307, 11: *12*, p. 319. This is explained by assuming that the deeper nephrons have not all been displaced on to the same higher initial collecting tubule. Thus, two branches are formed. This type seems to be the normal one in *Echidna* (Zarnik 1910).

It seems to me very probable that such a process of displacement of the peripheral junctions along the collecting tubules is, at least in a phylogenetic respect, responsible for the formation of the characteristics of the mammalian collecting tubules.

It is difficult to ascertain if the ontogenetic mode of development supports, or can be explained in accordance with this hypothesis. The

opinions on the development of the collecting tubules are very conflicting (cf. Peter 1927 c and Heidenhain 1923, 1937). With respect to the formation of the arcades there seems to be agreement, but the process of arcade formation as described by Peter (1927 c), though not conflicting with my view, gives no support to it, either. It might seem that the assumed displacement towards the periphery of the nephron junctions is in opposition to the opinions of Heidenhain (1923, 1937), who considers that a cleavage of the collecting tubules occurs in embryonic stages. It is, however, not impossible to think that such a displacement of the peripheral junctions may occur in addition to a cleavage of the collecting tubules.

The distribution of the typical arcades is of interest. They occur mainly in herbivores, especially the larger ones. In insectivores, carnivores and some small rodents there are seldom typical arcades. In *Arctitis* and *Ursus* there are, however, well-developed arcades (p. 324 and 328), as well as in *Pteropus* (p. 283). This indicates that the diet is of greater importance than the phylogenetic relationship in this respect. In this connection it may be mentioned that the initial collecting tubules are usually reduced in length or absent in nephrons joining arcades.

The thickness of the collecting tubules is probably also correlated with the mode of living. Generally it is smaller in carnivores than in herbivores, but exact information is lacking. Of special interest in this connection are the very thick collecting tubules in *Pteropus*, and the relatively thick ones in *Ursus*.

It is almost certain that typical arcades have been developed independently in several mammalian groups (e. g. *Megachiroptera*, *Ursus*, *Arctitis*, *Oryctolagus*, other rodents). This development has, of course, been facilitated by the fact that indications of arcades probably exist in all mammalian kidneys, and according to my view, that the process of displacement takes place already in the formation of the typical mammalian collecting tubule without arcade.

The cortical nephrons; long and short loops.

Peter (1909) has shown that cortical nephrons occur in *Sus* and *Homo*. Their occurrence is interesting, as they differ from the other nephrons in some important respects. The proximal tubules do not descend to the stripe boundary, the thin segment, usually confined to the inner zone and the inner stripe, may occur in the cortex, or be absent, the loops turn in the cortex, and usually the thick segment is not differentiated into a thicker and a thinner part. The cortical nephrons thus upset the whole structural scheme of the kidney. All the peculiarities they show

also exist in the embryonic stages of all nephrons (cf. Huber 1905, Peter 1927 b). From this fact it might perhaps be inferred that the existence of cortical nephrons is a primitive feature.

With regard to this the distribution of the forms with cortical nephrons among the mammals must be taken into account. Cortical nephrons in considerable numbers have hitherto been found in *Ornithorhynchus*, *Echidna* (Zarnik 1910), *Pteropus*, *Hystrix*, *Castor*, *Microtus*, *Evotomys*, *Arvicola*, *Arctitis*, *Elephas*, *Sus*, *Hippopotamus*, *Alces*, *Rangifer*, *Papio*, *Macacus*, *Homo*. A few cortical nephrons exist in the kidneys of the cow (some specimens), *Dama dama*, the horse according to Siewert (1927), and in one specimen of the rabbits examined by me. With the exception of the monotremes only forms feeding exclusively or mainly on plants have cortical nephrons. It may also be noted that most of them are relatively large forms (exceptions: *Pteropus* and the voles). As an insectivorous and carnivorous diet is certainly primitive in the mammals this distribution indicates that the occurrence of cortical nephrons, at least in the *Monodelphia*, is secondary and may be looked upon as a secondary retention of an embryonic feature. As regards the *Monotremata*, it is impossible to have a well-grounded opinion on this subject.

It seems also probable that in the *Marsupialia* and *Monodelphia* there are originally both long and short loops, i. e. the medulla consists primarily of outer and inner zone. Long loops are absent in *Hystrix*, *Castor*, *Elephas*, *Hippopotamus*, *Papio*, exceedingly few in *Ornithorhynchus*, *Echidna*, *Pteropus*, *Arctitis*, *Rangifer*, *Tragulus*, *Macacus sylvanus*. The long loops are few in *Microtus*, *Evotomys*, *Arvicola*, *Sus*, *Alces*. It is apparent both that the long loops are reduced in number in many herbivores but usually not in forms from arid habitats, and that there is a strong connection between the occurrence of cortical nephrons and the reduction of the long loops. It seems probable that the two latter features are, at least in part, consequences of a reduction of the thin segment (cf. p. 384).

In several carnivores all, or nearly all, loops are long (cat, dog, *Mustela*). The long loops are numerous in the other carnivores also, except in *Ursus* and to some degree in aquatic forms. The rodent *Psammomys* has only long loops. This preponderance of the long loops is shown macroscopically by the strong development of the inner zone, and is connected with the considerable length of the thin segment in these forms (cf. p. 388). The absence of short loops must also be considered as a secondary feature. The most primitive condition as regards the relation of long and short loops and cortical nephrons thus seems to be that still existing in the *Insectivora* and most small rodents, and in many other forms, too.

In this connection it may be noticed that those kidneys that contain

numerous cortical nephrons seem to have a very large cortex in proportion to the medulla. This is the case in *Sus*, *Rangifer*, *Alces* and *Elephas*, where the cortex forms about $^{9}/_{10}$ of the kidney volume. It seems very probable that all or most kidneys with such extreme cortical preponderance contain cortical nephrons in large numbers.

The dimensions of the nephron segments.

The length of the nephron segments.

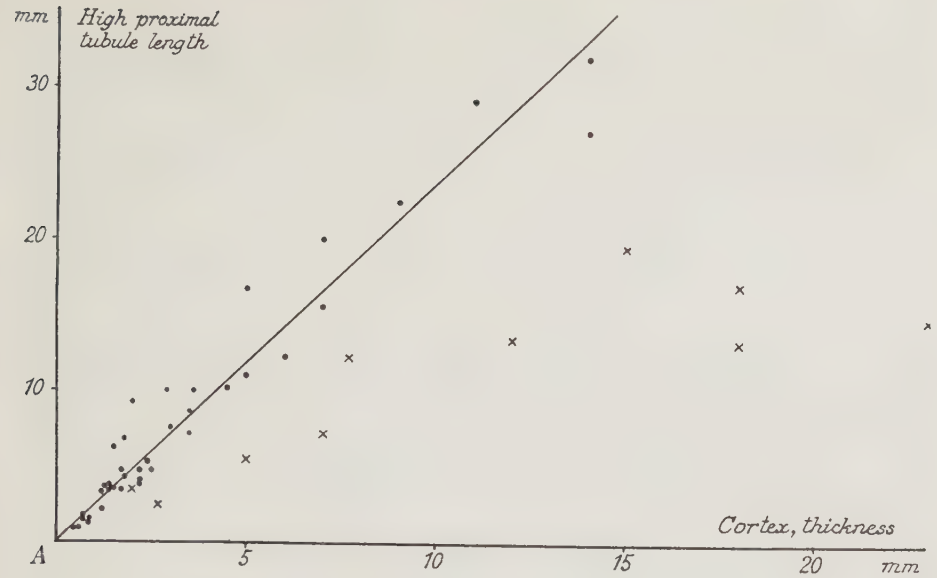
The proximal tubule. The nephrons and their segments usually vary considerably in length in the single kidney also. The proximal tubule is more easily studied in this respect than entire nephrons, owing to the difficulty of isolating the latter. A series of measurements has been made in *Mus flavicollis*, "young male", (table 22 a, b, p. 308), which is large enough to permit of a more detailed discussion of this subject. In this specimen there is no distinguishable difference in length between high proximal tubules and middle ones. Both categories show a moderate variation, and the measurements form a distribution not greatly deviating from the normal distribution. The deep proximal tubules, on the other hand, show a very skew distribution, and there are, perhaps, other irregularities in the distribution (though the material is not large enough to base definite conclusions upon it) with respect to the occurrence of more than one maximum. The mean length of the deep proximal tubules is distinctly higher than that of the higher ones. Taking all proximal tubules together, the distribution is also distinctly skew. This skewness is produced by the fact that a few of the deepest proximal tubules (and, indeed, all the corresponding nephrons) are much longer than the others. These longest nephrons have loops reaching or nearly reaching the area cribrosa, and are the first nephrons of the kidney to develop. In early stages of the kidney development they are, of course, much longer than the other nephrons, as is clearly shown in embryos and young (cf. Huber 1905, Peter 1927 c). In *Mus flavicollis* this relation is retained later, and in fact is demonstrable even in the oldest specimens examined. From the series of *Mus flavicollis* it might be inferred that the greater length of the deep nephrons is due not to their position and order of development but to the fact that they have long loops. It is, however, evident that the deepest nephrons in *Psammomys* (cf. also *Mustela*) are very much longer than the high nephrons, though in *Psammomys* there are long loops only.

Similar circumstances to those in *Mus flavicollis* are common. Thus, the deep proximal tubules are longer in shrews, bats and small rodents

(cf. also *Sminthopsis* and *Antechinomys*). There are, however, types where this is not the case. The dog may be taken as an example. Here, as is evident from the data p. 326, the deep proximal tubules are not longer, but shorter than the average. On the other hand, the high proximal tubules are the longest. As it is rather difficult to examine a great number of tubules in this species, owing to their comparatively great length, it has not been possible to obtain a clear picture of the length distribution of the deep proximal tubules. It is possible that the nephrons reaching the area cribrosa have proximal tubules decidedly longer than those of deep nephrons turning at a higher level. It is, however, certain that the distribution of proximal tubule length is quite different in the dog as compared with *Mus*. In the sheep the circumstances seem to be much the same. In the cow and the camel the high proximal tubules seem to be, relatively, still longer than in the dog. On the other hand the rabbit and the cat seem to hold a more intermediate position between the mouse and the dog in this respect.

It seems that almost all the small mammals have their proximal tubule lengths distributed according to the "mouse type". This is understandable if it is remembered that they have simple kidneys with a distinct papilla. The deepest nephrons have loops reaching the apex of the papilla. The longer the papilla is the longer these nephrons must be, and it is natural that the proximal tubules are lengthened with the nephrons. In cat and rabbit, for example, the papilla is not so long, relatively, as in the smaller types examined, and the deep nephrons are thus relatively shorter. This tends to make the longest deep proximal tubules relatively shorter, too. In types showing kidneys with a crest the depth of the medulla is further reduced (cf. p. 404). The length of the high proximal tubules is determined by the fact that they normally end at or near the cortico-medullary boundary. As the depth of the cortex increases proportional to the depth of the medulla, the length of the high proximal tubules is increased proportional to the length of the deep proximal tubules. This is what has happened in the "dog type".

The latter type is common among the larger kidneys. There are, however, a number of large kidneys which do not belong to this type, for instance the kidneys of *Sus*, *Elephas*, *Alces*, and probably some others. In these the high proximal tubules are distinctly shorter than the average, and the deep ones are at all events not shorter than the average, and usually longer. It is interesting to note that in all these kidneys there are cortical nephrons. In these nephrons the normal relations to the medulla have been lost, and as the proximal tubules do not reach the medulla they have the possibility of being shorter than might be expected from the thickness of the cortex.



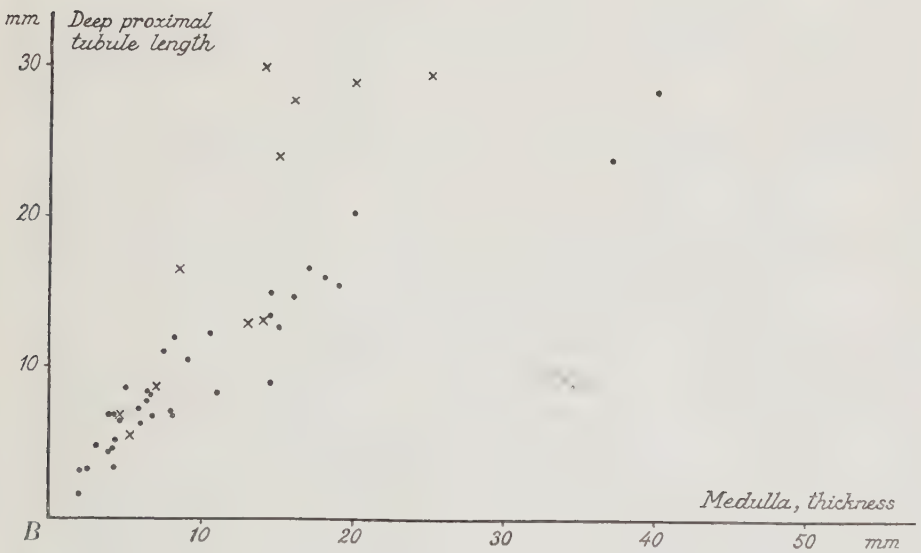


Fig. 24. Graphs showing the relation between proximal tubule length and thickness of the cortex and the medulla. In *A* the straight line through the origin represents the equation: Proximal tubule length = 2.4 × cortical thickness. The crosses represent in *A* kidneys with cortical nephrons, in *B* kidneys without or with few long loops.

These relations are shown in fig. 24 *A* and *B*. In fig. 24 *A* the mean lengths of the high proximal tubules in the examined forms are plotted against the thickness of the cortex. These quantities are directly pro-

portional in most species, but those species that have cortical nephrons diverge distinctly from the others. They also show a much greater variation. On an average the high proximal tubules are about 2.4 times as long as the cortex is thick, when there are no cortical nephrons.

In fig. 24 *B* the longest deep proximal tubule measured in each kidney is plotted against the thickness of the medulla. Here too, there seems to exist a linear relation between these quantities, except in kidneys where there are no long loops. The correlation between these quantities is, however, not so close, though this is probably due to random variation. It is, of course, difficult to find the longest tubules among the highly variable deep proximal tubules. Sometimes one of the longest has been found, but often this has not been the case. That the kidneys without long loops often have relatively long deep proximal tubules indicates that the proximal tubules in these cases constitute a greater part of the nephron length than in kidneys where the deepest nephrons have long loops. This is confirmed by the calculation of the composition of the deepest nephron in *Sus* (p. 351).

The thin segment. There is relatively little material available to show the mode of length variation in the thin segment. It is, however, clear that normally there is a distinct difference between nephrons with short and with long loops. In nearly all specimens where numerous nephrons have been measured the thin segment in short loops shows slight variation (shrews, small rodents). In long loops, on the other hand, the variation in length of the thin segment is great. There seems normally, or at least often, to be a distinct gap between the length distribution of short and of long loops. In kidneys containing cortical nephrons these relations are altered. The thin segment of the high nephrons is much more variable in length, and as there are often few or no long loops the distribution will be more continuous.

The thick segment seems in respect of its length distribution in the kidney to show two different conditions. In some cases the thick segments of the deep nephrons are about as long as or longer than those of the high nephrons (e. g. shrews). In other cases the thick segments are decidedly shorter in the deep nephrons. The former condition seems to be the rule in kidneys where the deep proximal tubules are much longer than the high. The latter condition, on the other hand, occurs where the deep proximal tubules are shorter or only slightly longer than the high ones. In both cases the ratio of the lengths of proximal tubule and thick segment rises the deeper a nephron is. The rising of this ratio seems to run parallel with the rising of the relative length of the thin segment. It seems reasonable to suppose that this is not accidental. It may be that the thick segment becomes shortened proportional to the

proximal tubule, because the thin segment is relatively lengthened. This view is supported by the fact that in kidneys devoid of long loops the thick segments of the deep nephrons are relatively long. The problem is, however, complicated by the fact that the thick segments of the high nephrons are not strictly comparable with those of the deep nephrons. The latter ones are entirely or almost entirely formed by the thicker part, whereas the high thick segments are formed by the thinner part also. In addition it must be mentioned that the cortical nephrons have relatively short, and often very short, thick segments, though they have no or very short thin segments.

The distal tubules seem on the whole to vary parallel with the proximal tubules, but their variability is often small. The difficulties in deciding where the distal tubules end are so great that it does not seem possible to say anything definite about them.

The diameter of the nephron segments.

The proximal tubule. In a kidney the longer proximal tubules are usually thicker than the shorter ones. This is evident from the tables of those species which show distinct length variations in the proximal tubules (e. g. bats, *Mus flavicollis* and *sylvaticus*, *Lutreola*, *Elephas*, *Alces*). Sometimes it is not possible to trace such a tendency, and sometimes the opposite condition is indicated, but this indication is so slight that it is impossible to show that it is not due to random variation. From the measurements it is also clear that the diameter of the proximal tubules is usually higher in kidneys with long tubules than in those with short. Thus it would seem that, generally, the diameter of the proximal tubules rises with their length. The diagram fig. 25 shows to what degree this is true. It is based on all measured proximal tubules from mature or nearly mature specimens. This material consists of two groups, those which have been examined fresh, and those which have been available only after preservation in alcohol. The former group has been treated as follows. In each kidney the proximal tubules have been classified according to their length after correction for swelling or shrinkage. The class interval is, for the shortest tubules, 0.5 mm (up to 4 mm tubule length), then 1 mm (up to 13 mm tubule length), and for the longest tubules the class interval is 2 mm. The mean diameter of the tubules of each class is calculated. When more than one specimen of a species have been investigated, the average of the means of the individuals is taken for each class. Each such class mean is represented by a cross. When alcohol material only has been available, the procedure has been the same, with the exception that a correction for shrinkage during

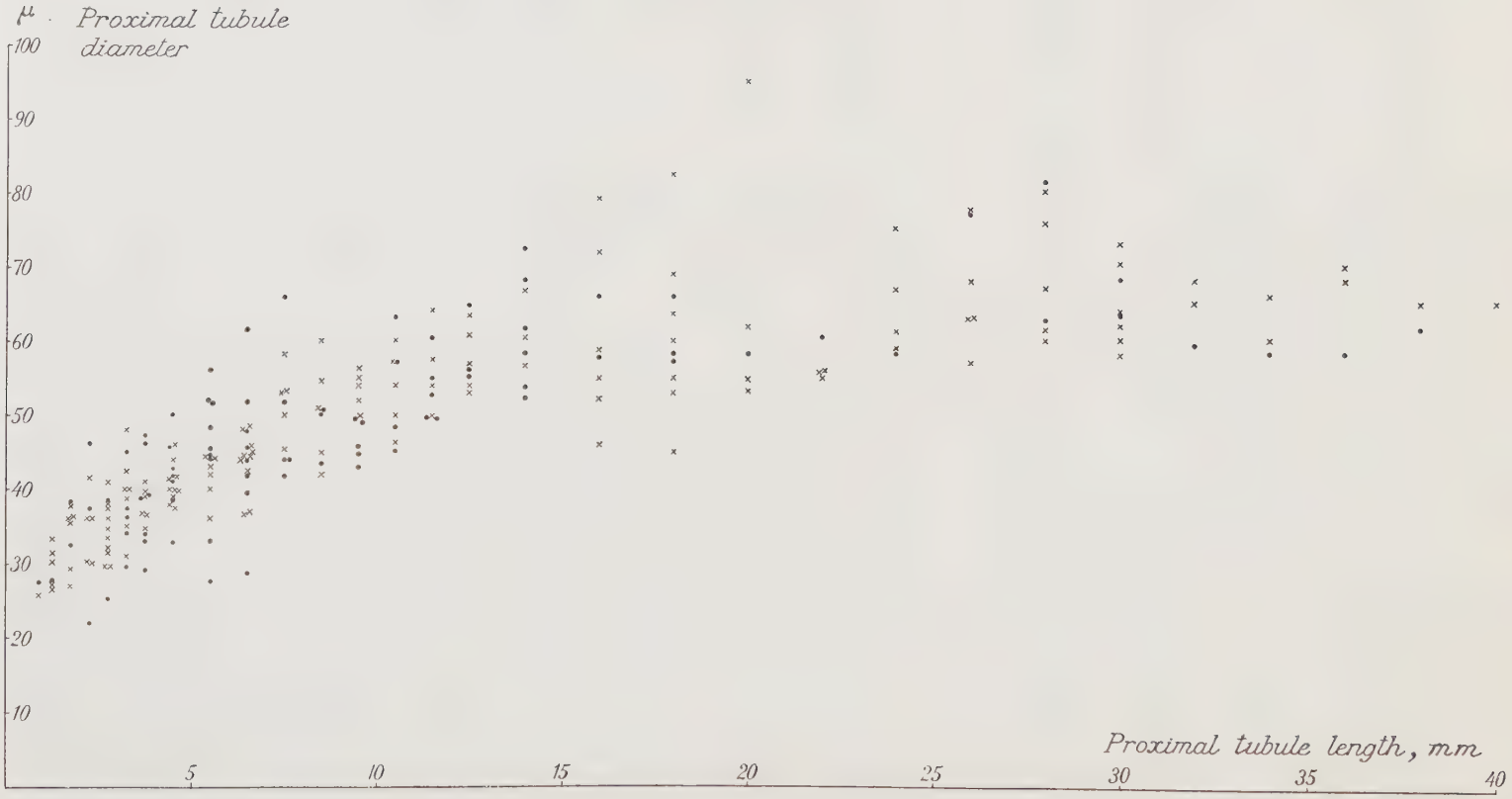


Fig. 25. Explanation see p. 379.

fixation has been introduced. Both the lengths and the diameters of the proximal tubules have, after correction for the shrinkage through maceration, been multiplied by 1.1. Then the procedure has been entirely the same as for the other tubules. The class means of each species have been represented by dots. It is evident that there is no great difference in distribution between the crosses and the dots. In fig. 26 *A* the classes have been put together, so that the class intervals are twice the original (except the end classes, which consist of three classes each) and the means of both crosses and dots together have been calculated. From fig. 25, and perhaps more clearly from fig. 26 *A*, it is evident that the diameter of the proximal tubules rises on an average fairly rapidly with the tubule length in short tubules. When tubules are longer than about 15 mm the rise in diameter is very slight when the tubule length is increased.

The relation between the outer diameter of the tubules in maceration specimens and the inner diameter of the tubules in the living animal is not known. It seems, however, almost certain that, in one kidney, tubules showing a large diameter after maceration must on an average have had a larger inner diameter in life than tubules showing a smaller diameter after maceration. The thickness of the tubule epithelium probably changes very little from one nephron to another. When kidneys from different species are compared it also seems that, on an average, the tubules which are thicker after maceration have in life had wider lumina. From this it seems reasonable to conclude that the lumen diameter of the mammalian proximal tubule rises relatively rapidly with rising tubule length in short tubules, but is only slightly altered in long tubules. That the diameter rises with the tubule length seems relatively understandable (cf. p. 408; the rise in intracapsular pressure caused by the increase in length is compensated by the rise in diameter). The limit for this rise is not so easily explained, but it seems probable that there is some connection with diffusion processes, and that, after a certain limit has been reached, the tubule becomes less effective as the lumen becomes wider.

Peter (1909, p. 299) thought the tubule thickness to be independent of tubule length. His relatively limited material did not allow of another conclusion. Conway (1937) finds this opinion probable on *a priori* grounds. He finds, however, from Peter's data a slight rise in diameter with rising body weight. This relation seems to be only a consequential one. In types where the tubule length is small and the body weight high the tubule diameter follows the tubule length (e. g. seals, whales).

In some species the tubule diameter is especially high in proportion to the length (bats, old cats, some pigs). This is probably due more to uncommonly thick epithelium than to great lumen width. In cats the epithelium often contains masses of "fat". In "Cat, male, kidney weight

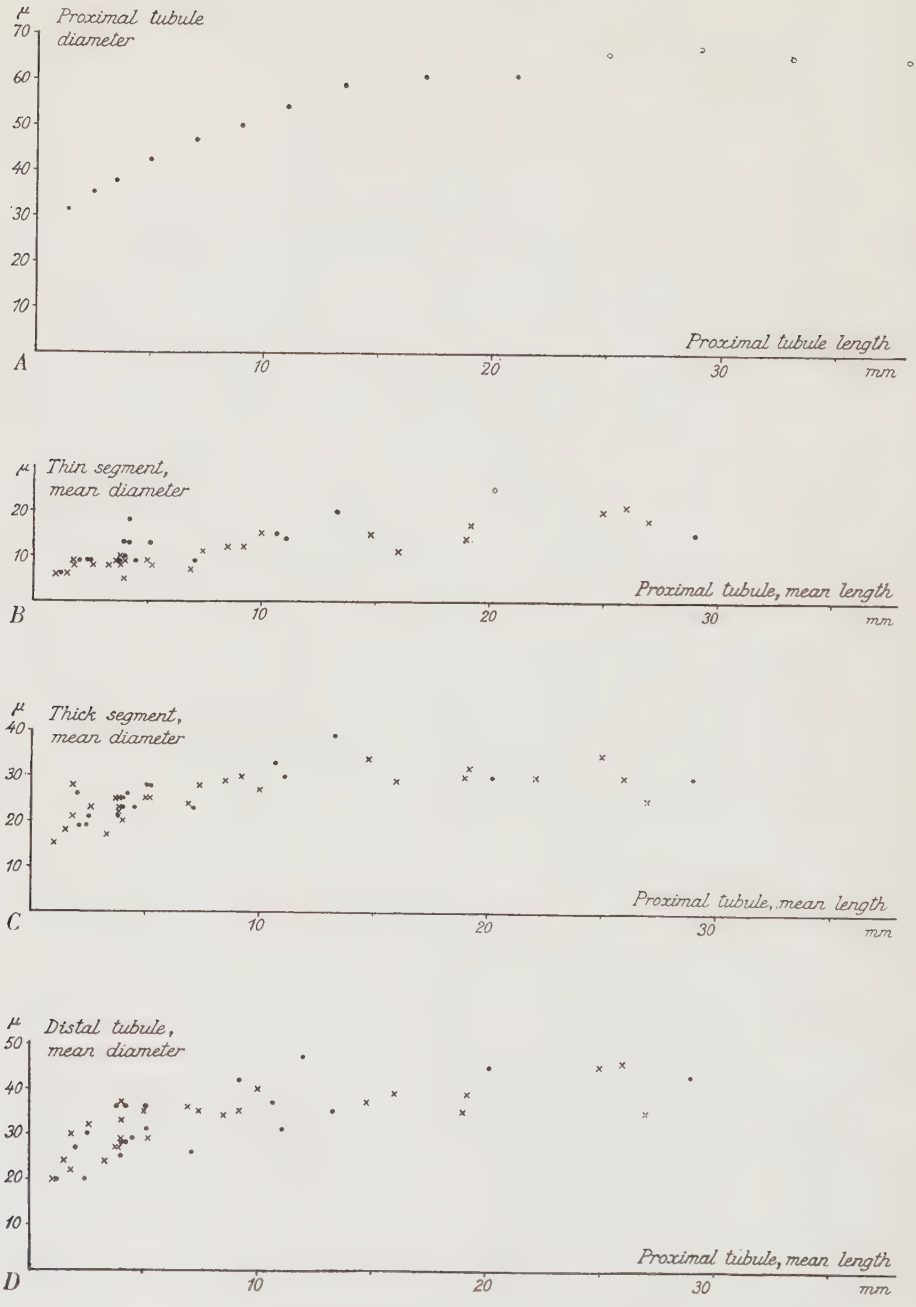


Fig. 26. Explanation see pp. 381—383.

17 gm", which had very thick proximal tubules, sections showed much higher epithelium than in a younger cat with normal tubule diameter. The latter showed about the same epithelium thickness as a rabbit

similarly treated. In *Pipistrellus* and the pig with great tubule diameter there was also a notable number of "fat" drops in the epithelium of the proximal tubules.

The thin segment. The proximal tubules show rising diameter with increasing length, also within one kidney. This is not the case with the other segments of the nephron. The thin segment is sometimes thicker in long loops than in short (*Psammomys*), but as a rule this difference is small, especially when regard is taken to the often very great increase in length. There is, on the other hand, a distinct increase in diameter when kidneys with long nephrons are compared with those with short. To show this the mean thickness of the thin segment in each kidney has been plotted against the mean length of the proximal tubule (fig. 26 *B*). Of course it would have been better if the mean length of the thin segment could have been used. The value of this is, however, usually unknown, and is relatively closely correlated with the mean of the proximal tubule. It is clear that the diameter of the thin segment increases distinctly with increasing nephron length, and probably more rapidly and continuously than the proximal tubule.

The thick segment. The same procedure has been used to get the diagram fig. 26 *C*. The diameter of the thick segment also rises distinctly with increasing mean proximal tubule length, and this in face of the fact that within one kidney the length of a thick segment is often inversely proportionate to the thickness. This is certain, at least in those kidneys where the thick segments of the deep nephrons are shorter than those of the high ones.

The distal tubule. This segment shows similar conditions to the thick segment, as far as different kidneys are compared (fig. 26 *D*).

With regard to the thick segment and the distal tubule it would have been possible to use the mean lengths of these segments instead of the mean length of the proximal tubule. The picture is then essentially the same.

The quantitative composition of the nephron.

The relation of the lengths of the segments.

The relative length of the different segments usually varies considerably from nephron to nephron in a kidney. This makes it difficult to obtain reliable figures for the mean composition of the nephrons, which represents the composition of the kidney with respect to the different segments. Only in a few cases has it been possible to calculate such figures. When this has not been possible there are, however, usually other data which permit a comparison between different forms. Usually

high and deep nephrons deviate in the same manner. This is evident when the figures for the composition of high and very deep nephrons are compared. Those kidneys where the thin segment is relatively short in the high nephrons also show this to be the case in the deep ones. This is also seen from the common occurrence of cortical nephrons in kidneys without long loops (cf. p. 374). That the thick segment in high and deep nephrons varies parallel is almost inevitable, as its length in both types is dependent on the thickness of the outer zone. Thus the composition of the kidney may, in a comparative sense, be judged by the composition of the high, deep or mean nephron, the occurrence and number of cortical nephrons and the relative proportion of long and short loops. Though the mean nephron is the best measure to use for comparisons the high nephron may well be taken when sufficient data for calculating the former are lacking. In each case the indications of the other data may be used in addition.

The examined forms may be divided into herbivores and carnivores (including the insectivores). *Arctitis*, *Ursus* and *Chiromys* are excluded, as the two former may be considered intermediate in this respect, and the diet of the latter seems not to be sufficiently known. There are data as to the composition of the high nephron in 17 species of the carnivore-insectivore group, and in 19 species of the herbivores (table 48, p. 419). The proximal tubule constitutes 39.9 ± 0.82 % of the nephron length in the former group, and 53.4 ± 2.18 % in the latter. Thus, the proximal tubules are relatively shorter in the carnivores than in the herbivores, and the difference is significant. The much greater variability in the herbivores is mainly due to the fact that some desert rodents (*Perodipus*, *Dipodomys* and *Jaculus*) have very short proximal tubules. The three more distal segments taken together are, of course, relatively longer in the carnivores than in the herbivores. This seems to be the case with the thin and the thick segment regarded separately, as well as with the distal tubule. The available material is scarcely large enough to allow of any estimation as to which is relatively longest in the carnivores.

The data as to the mean tubule composition are few, but they show that the two groups are as distinctly different in this respect as with regard to the high nephrons. The proximal tubule constitutes 37.6 ± 1.56 % of the mean nephron length in 7 carnivores and insectivores, and 52.9 ± 3.39 % in as many herbivores. The difference is 15.3 ± 3.71 % and is significant despite the small number of data.

The long loops seem on the whole to be more numerous in the carnivores. This indicates that the thin segment is shorter in the herbivores, and this is emphasized by the common occurrence of cortical nephrons among them.

In all respects *Ursus* and *Arctitis* resemble the herbivores, at least more than typical carnivores. *Chiromys* seems more like the insectivores.

The desert rodents, on the other hand, deviate markedly from the majority of the herbivores in most respects.

In the carnivore group the *Insectivora* seem to deviate by having relatively short thin segments. This is shown both in the high nephrons, the mean nephrons and the number of long loops. The *Microchiroptera* seem to be characterised by very short proximal tubules. The material is, however, so small that any attempt to subdivide the carnivore group must be very uncertain.

It may be mentioned that the two small insectivorous marsupials, which are not included in the above discussion, resemble the monodelphian insectivores closely.

The localisation of water reabsorption in the nephron.

In the above it is shown that the composition of the nephrons is different in herbivores and carnivores. As there is a general difference in the composition of the urine between these groups this indicates a parallelism between the quantitative composition of the nephrons and their function. It is, then, possible that a comparison between the composition of the urine and the nephrons may help to localise the processes in the nephrons.

This problem has been solved, in the *Amphibia*, at least in its essentials, by direct methods (cf. Richards 1938). In the mammals some of the most important problems concerning the function of the proximal tubule have been solved by Walker, Bott, Oliver and MacDowell (1941), also by direct methods. (Since the terminal segment may possess other functions than the preceding part of the proximal tubule, which is the part investigated, the assumption that their results are valid for the whole proximal tubule does not seem warranted.) These authors have also attempted to analyse fluid from the distal tubule, but they do not consider the available material sufficient for any conclusions. The other segments of the nephron do not seem accessible to their technique.

Several authors have attempted to make clear the functions of the different parts of the nephron in the mammal by studying the excretion and distribution within the nephrons of dyes (e.g. Heidenhain 1874, Bensley & Steen 1928, Holton & Bensley 1931, Edwards 1933, Gersh 1934, 1936, Gersh & Stieglitz 1934, Kempton, Bott & Richards 1937, Ellinger 1940) or substances normally excreted (e.g. Glimstedt 1942). The results of these investigations seem often very difficult to interpret, and are often conflicting.

In some cases a comparison between structure and function of the kidney in different forms has been used to localise the processes in the nephrons. A survey of this method and its results has been given by Marshall (1934, 1935).

Pütter (1911, 1926) has attempted to build an entire theory of kidney function on a comparison between the volume and composition of the urine, and the nephron composition. To that end he has evaluated Peter's measurements quantitatively. His methods and results show the danger of such a proceeding when the material is inadequate (cf. p. 390). Pütter's hypothesis has received little attention (cf., however, v. Möllendorff 1930).

Another theory, based on a comparison between physiological and anatomical facts, seems to have been generally accepted. This theory has been most fully formulated by Burgess, Harvey and Marshall (1933) and Marshall (1934) (cf. Starling & Verney 1925, Crane 1927, Korr 1939). It maintains that the hypertonicity of the urine as compared with blood arises in the thin segment, the latter reabsorbing water under the action of pituitrin.

The main facts supporting this theory are the following:

1. The thin segment is typically developed in mammals and birds only.
2. The water reabsorption is increased by pituitrin in mammals and birds.
3. The urine may be hypertonic only in mammals and birds.

The basis for this theory is not very broad. Point 1 may be considered established, though it is not impossible that there are some reptiles not yet examined, which have thin segments. Points 2 and 3 are based on the examination of a few forms, and these forms do not seem significant in this respect. That such a freshwater form as *Alligator* does not respond to pituitrin with increased water reabsorption is no proof of the general inability of reptiles to do so. There is, of course, no need for freshwater animals to develop or retain a mechanism for conserving water. It is possible that the reptiles are able to conserve enough water without forming hypertonic urine, even when living in arid habitats or in the sea. As long as such forms have not been thoroughly examined it cannot, however, confidently be said that the reptiles lack this capacity.

In the bird kidney most nephrons have no thin segment, and many of the thin segments existing are very short (Lindgren 1868, Huber 1917, Feldotto 1929, my own investigations, unpublished). If, under the influence of pituitary extract, water is reabsorbed in the bird kidney by the thin segment only, most of the nephrons either do not function in this case or they form hypotonic urine.

According to Gibbs (1929 a, p. 59) the uric acid may amount to 17.5 % of the weight of the ureter urine in the fowl. The urine is then "sticky, solid" (Gibbs 1929 b, p. 598). It seems impossible that this urine, formed under the influence of pituitrin, could be a mixture of a little concentrated portion from the nephrons without thin segment and a more concentrated portion from the nephrons with it. The latter portion would then be so concentrated as to be entirely solid. Under the action of pituitrin the output of uric acid is considerably increased, which makes it very improbable that only a part of the nephrons is functioning.

Nor when the bird kidney forms a watery, but osmotically concentrated urine (Kore 1939) does it seem probable that only the nephrons with thin segment are at work. If all nephrons are functioning this would mean, according to the above theory, that some of the nephrons produce a highly concentrated fluid, which is then very much diluted by the admixture of dilute urine from the majority of the nephrons. This does not seem probable.

It must, then, be concluded that it is not probable that the water reabsorption in the bird kidney, influenced by pituitrin and leading to hypertonicity of the urine, takes place in the thin segment only.

It is somewhat doubtful if this conclusion has any bearing on the same problem in the mammals. The thin segment is undoubtedly homologous in birds and mammals, but this does not necessarily mean that the function is identical in both groups. As the structure is very similar it seems, however, most likely that the function is so, too. It may then be inferred that the thin segment of the mammalian nephron is probably not the place where the hypertonicity of the urine arises.

Peter (1909, p. 335 et seq.) states that the thin segment is better developed in mammals with concentrated urine, and infers that the thin segment is the portion of the nephron which concentrates the urine. Peter's material seems to be too small to allow of any definite conclusions in this respect. Nor has he attempted to discover if any other segments show similar conditions.

It seems possible that the material now available can be used to examine the problem with greater prospects of reaching well-founded conclusions. A great difficulty is, however, the scarcity of comparative physiological data, even with respect to the osmotic concentration of the urine. Thus, it is necessary mainly to rely on conclusions drawn from the mode of life of the forms in question.

It is well known that the urine of carnivores and herbivores is very dissimilar in many respects. In the former the urine is usually more concentrated and acid, and there are many other differences too (cf., e. g., Chaussin 1920, Noll 1924, Fuse 1925, Pincussen 1925, 1934). Thus, it

is difficult to draw any conclusions as to the localisation of distinct processes from a comparison between herbivores and carnivores with respect to urine and nephron composition.

The problem seems somewhat simpler if more similar forms are compared. It is shown by Howell and Gersh (1935) that *Dipodomys* has very concentrated urine. This is certainly also the case with the other desert rodents examined, *Perodipus*, *Jaculus*, *Psammomys* (table 48). The ratio of the mean lengths of the proximal tubule and the thick segment is in these four forms 1.18 ± 0.106. Some other small rodents, which seem comparable to the above except in not being desert forms, have been examined, namely *Sciurus*, *Epimys rattus*, *Mus musculus*, *flavicollis* and *sylvaticus* and *Microtus agrestis*. The ratio of proximal tubule and thick segment in this group is 2.00 ± 0.051. The difference is 0.82 ± 0.118 and is significant despite the low number of data. It is not possible to make a similar comparison for the mean length of the thin segment, as there are no figures for it in *Psammomys*. There can, however, be little doubt that the thin segment is also relatively longer in the desert rodents than in the normal small rodents.

There are no detailed investigations concerning the excretion in the desert rodents, and there is also no complete knowledge of it as regards the other small rodents. It is thus impossible to say quite definitely that the concentration is the only difference between the urine of these forms, though it seems probable that it is the most important one.

The camel, which excretes a concentrated urine, apparently has longer thick and thin segments than the cow.

Little is known about the urine of the shrews and the bats. It seems reasonable to assume that they are similar, except that the bats should be expected to excrete a more concentrated urine, as they certainly lose relatively great quantities of water during flight (cf. Eisentraut 1937, p. 66). Both the thin and the thick segment seem to be longer in the bats.

Pachyura, which lives in drier habitats than the other shrews examined, shows relatively longer thin and thick segments than they do.

The carnivores seem to have, on the whole, more concentrated urine than most herbivores. The thin and the thick segment are relatively longer in the carnivores.

In the seal the osmotic concentration has been found not to exceed that occurring in terrestrial carnivores (Portier 1910, Irving, Fisher & MacIntosh 1935, Smith 1936). This is certainly also the case in those whales that feed on vertebrates. The urine has been examined in dead whales, and the freezing-point depression has been stated to be moderate (Schmidt-Nielsen & Holmsen 1921, Morimura 1925, Suzuki

1925). It would seem, however, that the forms feeding on invertebrates are constantly forced to excrete large quantities of osmotically concentrated urine, as their food contains much osmotically active substance, and is probably mixed with sea water. In *Balaenoptera* the thick segment is unusually long, but the thin segment seems to be rather shorter than in most carnivores.

From the above it seems that the thick and the thin segment are normally longer in animals excreting a concentrated urine than in other forms. This indicates that both segments are connected with water reabsorption. The relative shortness of the thin segment in *Balaenoptera* suggests that the thick segment is more essential in this respect than the thin segment. (*Hystrix*, which lives in relatively arid habitats, has short thin segments, as shown by the absence of long loops, which may also indicate this. As there are no investigations of the urine of *Hystrix*, and its habits do not seem sufficiently known, this case may be considered doubtful.)

It is clear that if both the thin and the thick segment participate in water reabsorption, the thin segment cannot be the main place where the hypertonicity of the urine occurs. It seems more reasonable to assume that water, and perhaps also solutes, are reabsorbed from the fluid in the thin segment not against, but along with the concentration gradient. The structure of the thin segment seems well suited to a more passive exchange of this kind through its walls. The reabsorption against the concentration gradient would then occur in the thick segment. It must, however, be remembered that the data presented here do not exclude the possibility of the distal tubule sharing the reabsorptive capacity with the thick segment. On the contrary, this may well be the case, and it does not seem impossible that at least some part of the collecting tubules is similarly active[1].

The carnivores, and doubtless the insectivores also, excrete an acid urine in contrast to the herbivores. This may be connected with the fact that these groups have longer distal tubules than the latter (cf. Ellinger 1940). It is, however, doubtful if this difference between carnivores and herbivores is in reality so marked as it might seem, as the distal boundary of the distal tubule is almost always difficult to distinguish, and possibly the last segment of the distal tubule sometimes forms a part of the arcade. The distal tubule is usually thicker in the herbivores, also.

[1] This view is consonant with most of the investigations on the excretion of dyes.

The surface area and the volume of the nephrons.

The surface area and the volume of the glomeruli have been estimated by several authors (e. g. Saéki 1926, Vimtrup 1928, Rytand 1938).

The measurements of Peter (1909) and Inouye (1909) have formed the basis for some attempts to calculate the surface area of the different segments of the nephron and the total surface area of the nephrons (Pütter 1911, 1926). The investigations of Peter and his co-workers aimed primarily at a thorough knowledge of the qualitative structure of the kidney. This is no doubt the reason why only a relatively small number of measurements have been made by them. These measurements are not a sufficient basis for such a detailed quantitative analysis as that attempted by Pütter. Peter's material has often shrunk considerably, as he sometimes mentions. As an example of the very serious errors introduced when the shrinkage is not taken into account, the following case may be mentioned. Pütter (1926, p. 95) gives the kidney weight of the rabbit as 13 gm and the number of the nephrons as 285 000 (op. cit. p. 91). The average nephron he calculates from the data given by Peter has a volume of almost 0.01 cmm. The joint volume of all nephrons is then not over 3 ccm. As the nephrons form at least $^3/_4$ of the volume of the kidneys (cf. Glimstedt 1942) this value is less than a third of what it ought to be. The main reason is undoubtedly that Peter's material has shrunk. If the calculation is otherwise correct (i. e. the nephron number the same in the rabbit kidneys used by Peter and Pütter), which is possible, but not certain, the surface area calculated by Pütter is about half the correct value. When figures with such doubtful value are used as absolute and are then correlated with equally uncertain physiological data, such a procedure can only discredit quantitative anatomy.

As I have not measured the nephron number, my measurements of the nephrons are not suited to calculations of the absolute total surface and volume of the nephrons. I have, however, in table 49, p. 422, given the relative surface and volume of the segments of the average nephron in some species, where fairly reliable estimates of the dimensions of the average nephron have been obtained. In these cases the average nephron number of the species has also been given, when reliable data exist. The product of this number and the nephron volume should approach the kidney volume. The agreement is fairly good. When calculating the percentage of the segments the capsule has been excluded, as its relative size varies greatly and to some extent obscures the regularity of the nephron composition in other respects. Among the other nephron components the thin segment and the distal tubule show the largest varia-

tion. This is undoubtedly to some extent due to errors of estimation, as these parts are more difficult to examine quantitatively than the others. The thin segment is, however, undoubtedly very variable, as is shown by its varying relative length in the high and mean nephrons (table 48). Table 49 brings out distinctly how small a part of the total nephron surface and volume is formed by the thin segment. Even in *Dipodomys*, where it is uncommonly developed, it does not seem to form more than 5—6 % of the nephron volume. This is still more striking when regard is taken to the fact that, of this volume, the epithelium forms only a small part, certainly less than 20 %. As, in the other segments of the nephron, the epithelium forms the greater part of the volume, the epithelium of the thin segment probably constitutes less than 1 % of the epithelium volume of the kidney in most cases, and very often, in herbivores, less than 0.5 %.

The surface index. v. Möllendorff (1922, 1930) has examined the relation between the surfaces of the proximal tubule and the glomerulus. This relation, the "Nierenindex", is obtained by multiplying the capsule surface by 3 (or, in the mouse, by 1.3) to obtain the glomerular surface, and dividing the surface of the proximal tubule by the product. Apart from the factor 1/3 this index is the same as that given by me in the tables under the heading "Ind.". One of the difficulties of this line of thought is evident at once. The purpose is to give a ratio of the reabsorbing and the filtering surfaces of the kidney. According to v. Möllendorff the glomerular surface should then be proportional to the capsule surface in the mammals (except in the mouse). According to the conceptions on which Vimtrup (1928) has founded his estimations of the glomerular surface, this surface is proportional to the volume of the capsule (when the diameter of the blood-capillaries is constant). This is also in accordance with Nash (1931). Still another difficulty (emphasized by v. Möllendorff 1922) is that the *inner* surface of the nephron and not the *outer* must be considered as the reabsorbing surface. These surfaces are undoubtedly not strictly proportional (cf. p. 381).

It would thus seem that the following ratios might be regarded as estimates of the ratio of the reabsorbing (or secreting) and filtering surfaces, as well as v. Möllendorff's index: 1. The ratio of the surface of the proximal tubule and the volume of the capsule. 2. The ratio of the volumes of the proximal tubule and the capsule. 3. The ratio of the length of the proximal tubule and the surface of the capsule. 4. The ratio of the length of the proximal tubule and the volume of the capsule.

The relative size of the capsule is very varying, also within the species and even within the kidney. The capsule is certainly larger when the glomerulus is distended with blood than when it is empty. It seems very

probable that the capsule reacts differently and probably within wider limits than the other parts of the nephron when the material is swelling or shrinking. During dissection and measuring the capsule is more liable to deformation than other parts (cf. p. 261). All these factors make the data on the size of the capsule far less trustworthy than those on the other parts of the nephron. This explains, at least in part, the sometimes extreme differences within the species between the indices of different specimens (e. g. *Microtus*, p. 301, 302) and the great variability normally occurring within each kidney. This fact diminishes the importance of this index. It is, however, fairly constant when the indices of mammals of different size and habit are compared (table 48, p. 419). This might indicate a special significance for it. I have calculated the ratios 1—3[1] for each species also, and the ratios 2 and 3 are constant in the same sense and to the same extent as the index. The ratio of the surface of the proximal tubule and the volume of the capsule seems to diminish with increasing tubule length, but apart from this the variability is not greater than in the index. Thus, a comparative review of the index in the mammals gives us no reason to suppose that it is an especially important "constant" for the kidney.

v. Möllendorff has tried to show that the index is constant within the kidney (apart from random variation). This is sometimes true, but in other cases the index is higher in high nephrons than in deep (e. g. *Mus flavicollis*, "young male", table 22 c, p. 309). The contrary seems to be true in some cases (*Sminthopsis murina*, p. 267, *Pachyura etrusca*, p. 280, *Pipistrellus nilssoni*, p. 284). Though I have not made any detailed investigation in this respect, it does not seem that the ratios 1—4, given above, show definitely less constancy within the kidney, than the index.

v. Möllendorff assumes that the index is low in aquatic mammals, and ought to be high in desert forms. This seems not to be the case. The index is not higher in the desert rodents than in normal forms, and there is no significant difference in this respect between the aquatic forms and terrestrial mammals. As far as the values indicate anything, it might seem that the ratio of the surfaces of the proximal tubule and the capsule is not correlated with the concentration of the urine. This would seem to mean that the reabsorption in the proximal tubule is not correlated with the final concentration of the urine. Such a conclusion is, of course, very uncertain.

[1] The ratio 2, the "volume index", has been calculated from the means of the tables by dividing the product of the square of the diameter and the length of the proximal tubule by the cube of the diameter of the capsule. The figure thus obtained is multiplied by 1.5. An equivalent of the ratio 1 has been obtained by dividing the "volume index", and of the ratio 3 by dividing the "index" by the diameter of the proximal tubule.

Age changes in the kidney.

In the present investigation no consistent examination has been made of the differences in kidney structure due to age differences. In some species small young have been examined in addition to mature specimens of different ages. In other cases the age of single specimens has been known or estimated. This material allows some notes on this subject.

The kidney form sometimes shows modifications in this respect. In the cat the newborn young can hardly be said to have a prominent papilla. The papilla then becomes more prominent, but in the oldest specimen a reduction of the prominence has probably taken place (fig. 11, p. 319; cf. also Marschner 1937, p. 376). Such a process is probably at work in other *Felidae* also (*Lynx*, lion). The cause of this is that, in the young, the medulla grows, which makes the papilla project. Later the increase in depth of the medulla stops, but the cortex, and to some degree the outer zone, increase in volume. This increase is not a simple enlargening of the outermost parts; growth takes place in the inner parts also, and apparently in all directions. Thus, the cortex expands parallel to the surface also, the base of the medulla is obliged to follow this expansion and the papilla is partly drawn in.

The continued growth of the cortex and outer zone, and the cessation of increase in depth of the inner zone, seem to be a common phenomenon. It is evident in the rabbit and *Mus flavicollis*, and the data as to the cow and Man (Toldt 1874, Peter 1927 c) indicate its presence. The macroscopic modifications are, however, small in most mature mammalian specimens. That the cat shows so distinct modifications seems to be due to the fact that the cat kidney is enlarged in old males (cf. Hall & MacGregor 1937).

As there is no formation of new nephrons after the earliest postembryonic stages, the growth of the kidney depends on the growth of the tubules. These increase in length as well as in thickness (rabbit table 13, pp. 290—292, *Mus flavicollis* table 22, pp. 308—311, cat table 26, pp. 321—324, cow table 44, p. 358). If there is no increase in the diameter of the tubules the length of the nephrons will be directly proportional to the kidney weight, provided there is no material change in their composition. If the growth is equal in all dimensions of the nephrons, the increase in length will be proportional to the cube root of the kidney weight. It seems probable that in reality the increase in nephron length will lie between these extremes, but there is not enough material available to show exactly the conditions in any species.

The proportions of the nephron are not constant during growth. The proximal tubule constitutes about 30 % of the nephron length in the

12-day-old kitten, some 30—35 % in the young female cat and about 45—50 % in the old male (pp. 320—321). Quite similar conditions are found in the rabbit (p. 292) and the cow (p. 358). In all of them the proximal tubule is relatively short in the very young specimens. Except in the cat it does not seem that the composition of the nephron is distinctly modified with age in mature specimens (rabbit, *Mus flavicollis*), except that the thin segment probably does not increase as fast as the other segments, as the inner zone is relatively little increased.

In the kitten there are a great number of short loops, but in the older specimens there are none, or very few. Similar circumstances must exist in all forms with long loops, as in an embryonic stage there are generally only short loops. The development of short loops into long takes place at an early stage in post-embryonic life, as there is a relatively constant ratio of short and long loops also when young specimens are included, in rabbit, *Mus flavicollis*, cat, and cow.

The segments of the nephrons become more tortuous in old specimens, probably as a consequence of growth. This is especially the case with the proximal tubule, in which the pars recta also may become very tortuous (rabbit, Pl. 1, fig. *4*; white rat, Pl. 1, fig. *5*). The distal tubule seems often to be more irregular, and its surface has more marked projections in old specimens.

It may be mentioned that the old kidneys often contain much very tough connective tissue, which together with the greater length and more tortuous course of the tubules makes it very difficult to obtain satisfactory preparations from them.

The form of the mammalian kidney.

Survey of the literature.

The problems concerning the form of the kidney, especially the relation between the simple kidney and the renculi kidney, have been discussed by many writers.

Hunter (1787) correlated the renculi kidney with water-life. This notion has later been discussed and accepted by Cuvier (1840) and Daudt (1898). As Gerhardt (1911) points out this correlation is not so close as was assumed by earlier writers. He also shows that there is no connection with hibernation, as had been assumed by Cuvier. Many aquatic animals have smooth kidneys (*Castor*, *Fiber*, *Lutreola*, *Halicore*), and many terrestrial forms have lobated kidneys (*Elephas*, *Ursus*, *Bos*). This problem has also been discussed by Anthony (esp. 1919), who assumes that the renculi kidney is dependent on two factors: 1. Such

factors that intensify urine formation (life in cold climate, water-life, absence of sweat glands), 2. Body volume. The larger an animal is and the more active the factors mentioned under 1. are, the larger its kidney surface will tend to be. This hypothesis pays no regard to features of kidney structure other than the surface, and the theory behind it is erroneous. ANTHONY (and before him DAUDT 1898) assumes that the surface augmentation is called for by increased urine volume. Indeed, he says that the secreting surface must be increased. The kidney surface has, however, no demonstrable relation to the secreting surface of the kidney. As no other types than the renculi kidney are considered there are also numerous exceptions to the rule given by ANTHONY. Anyhow, his theory marks an advance, as it takes into consideration the important factor of body size.

PETER (1909), HOLLATZ (1922) and v. MÖLLENDORFF (1930) assume that the relation between the volumes of the cortex and the medulla is the deciding factor with respect to kidney structure. The larger the cortex is in proportion to the medulla the more the kidney ought to be divided into lobes. From the investigations of DENZER (1935) it is evident that this is not the case.

ZARNIK (1910), gives another view on this problem. He assumes that there is an upper limit for the length of the nephrons (op. cit. p. 145). The nephrons must be distributed within the kidney in such a manner that, in large kidneys too, this upper limit is not exceeded. This may be accomplished by the dividing of the renal substance into renculi in large kidneys, or by the elongation of the kidney in those with tubi maximi. Thus, his theory in the first place attempts to explain the derived kidney forms in large animals, but he points to the probability that this upper limit for the nephron length may be different in different circumstances.

The opinion of ZARNIK has, to my knowledge, been cited only by FREUND (1912). In his paper of 1939, however, he does not mention it. Other authors seem not to have regarded it at all. The reasons for this are probably the following. The formulation of ZARNIK's theory is very short, and there are no reasons given as to why there should be such a limit. Neither are there any investigations to show that there is any real connection between kidney type and nephron length. Another obstacle to its wider recognition is probably that it is printed as a small part of a chapter on "Beziehungen der Echidnaniere zu der Niere der höheren Säugetiere". I myself did not find the passage before my opinions in this respect had already been worked out.

On the whole it may be said that, hitherto, none of the opinions advanced as to the relation of the kidney types to environmental or

other factors has been generally accepted. Most of them have only considered the difference between simple and lobated kidneys. This uncertainty as to the factors at work is also expressed by the latest handbooks (v. Möllendorff 1930, p. 262, van den Broek 1938, p. 831, Freund 1939, p. 89).

The problem of the relation between mode of life and kidney form has thus been discussed very early on, and it has later usually held a central place in the interest of kidney investigators.

This is perhaps the reason why most authors have been relatively little interested in the question as to which kidney type is primitive in the mammals. It is seldom that clear opinions on this subject are found. This is quite natural for the pre-Darwinian writers, but is somewhat remarkable in later authors.

The simple kidney has been considered primitive by Gegenbaur (1901) and Gerhardt (1911, 1914). None of them says this in so many words, but it is evident from their arrangement of the kidney types. A certain obscurity is, however, caused by their erroneous conception as regards the kidney of the *Monotremata* (cf. p. 265), which Gegenbaur considers to show sauropsidan features (op. cit. p. 467).

Zarnik (1910) is led to think that the simple kidney is primitive by his study of the *Echidna* kidney.

The contrary view seems to be held by Freund (1912), as he speaks of "verschmolzene Nieren", but he does not state this direct. In 1939 he only gives the two opposing theories without defining his own point of view.

Mijsberg (1923) considers the human kidney primitive as compared with the simple kidneys of the monkeys (but in 1931 he seems to have altered his opinion). The same opinion is held by various authors studying the position of Man among the mammals (Bolk 1921, Wood Jones 1929, Westenhöfer 1942).

Ellenberger and Baum (1926) assume the renculi kidney to be primitive, as does Zuber (1935).

With respect to these very divergent opinions it is natural that the authors of handbooks, e. g. Weber (1927), v. Möllendorff (1930) and v. d. Broek (1935), hesitate to give any definite opinion on this subject.

Those authors who think the renculi kidney to be primitive seem to do this for two reasons. The most important of these is the belief that embryology supports this view. This subject is treated on pages 397—399.

The other reason is that in many cases the surface of the kidney is grooved in embryonic stages and also in early post-embryonic life, but becomes smooth with age. This is especially the case in Man, but occurs also in the cow, the elephant and possibly in other forms with lobated

kidneys. This has been taken to indicate that a real fusion of lobes, leading to simple kidneys, has occurred. This is not the case; the modification is entirely superficial (cf. p. 345 and p. 356). This view has had the more influence as the interest of the authors has centred around the contrast smooth — lobated, leaving other conditions out of account.

The embryonic development of the form of the mammalian kidney.

It seems that most of those authors who incline to the view that strongly lobated kidneys are primitive in mammals do so on the assumption that embryology supports such a view. Below I will shortly examine this matter. This is necessary mainly because some authors, to my knowledge Ellenberger and Baum (1926, p. 511), Hahn (1921), Zuber (1935), Hertwig (1910, p. 502), and Kingsley (1917, p. 369), plainly state that the kidneys of all mammals are lobated during the embryonic stages. None of them gives any report of any personal investigations to support their statements, or any reference to the papers of other authors on this subject. Thus it is difficult to say how they may have come by this opinion. However, the statements as to this subject are so widely scattered in the literature of kidney embryology, and Felix in Hertwig's handbook (1906) gives such brief information on the matter, that it is difficult to reach a well-founded opinion without personal investigations or relatively extensive studies of the literature in question.

Felix (1906) does not discuss this matter separately, but from the following passage (op. cit. p. 344) it is evident that, in his opinion, simple kidneys are not lobated during their development: ". . . beschränkt sich die neogene Zone der einfachen Niere auf die Peripherie des Gesamtorganes". On the other hand he writes concerning the lobated kidneys: ". . . bei der zusammengesetzten Niere zerfällt die neogene Zone in mehrere . . . die neogenen Zonen breiten sich infolgedessen nicht bloss an der Peripherie der Niere aus, sondern dringen bis zum Nierenhilus vor und scheiden dadurch die ganze Nierenanlage in die verschiedenen Renculi." This is almost word for word what Rathke (1861) has written on this matter (cf. also Toldt 1874, p. 132).

I have not been able to find any statements on this subject referring to embryos of monotremes or marsupials. In three embryos (or pouch young) of *Didelphys* (kidney lengths 2.4 mm, 5.5 mm and 8 mm) there is no sign of superficial or internal division, and a papilla is developed. The case is the same with an embryo of *Philander sp.* (kidney length 1.7 mm). In an embryo of *Phascolarctus cinereus* and one of *Choeropus* (kidney lengths 8 mm and 6 mm) the medulla is also undivided, but no

papilla is developed; in the latter some slight furrows can be seen on the surface, but without causing any division of the cortex.

I have examined some embryos of insectivores and bats, but I have not found any statements in the literature. At most there are very slight furrows on the surface, and there is no division of cortex or medulla. (Examined are *Talpa* embryos with kidney lengths 0.8 mm, about 1.1 mm, 2.6 mm; *Erinaceus* embryos, kidney lengths 1.5, 2.8 and about 5 mm; a *Centetes* embryo with kidney length 1.3 mm; *Myotis* and *Plecotus* embryos, kidney lengths 1.0 and 4 mm).

Concerning the rodents there are statements by several authors. It is quite clear that the kidneys of the following are never lobated: Rabbit (Löwe 1879), rat and mouse (Hamburger 1890 and Chiewitz 1897), *Spermophilus* (Völker 1922). In addition to this I have examined several embryos of rabbit, *Mus* and *Microtus*, and have never found any traces of a real division, but only occasional, superficial grooves.

There seems to be little information as to carnivores in the literature. Toldt (1874) gives some figures of kidney stages of cat and dog. No division is shown. In a series of five cat embryos (kidney lengths 1.3 mm, 4.5 mm, 6.5 mm, 7 mm, 9 mm) the kidneys are smooth exteriorly, and both cortex and medulla are undivided. There is no papilla.

In *Equus* (Schurian 1925) the kidney is at first quite smooth and undivided. Later, several grooves appear, but mostly they disappear before or after birth. Schurian did not investigate the interior structure, but it seems most probable that the medulla is always undivided (cf. Chiewitz 1897). This is the case in a horse embryo that I have investigated (kidney length 25 mm). As previously (p. 365) mentioned, a *Diceros* embryo has strongly lobulated kidneys.

Concerning *Sus* the statements are divergent. Toepper (1896) and Hauch (1903) state that the kidneys are undivided exteriorly, but Toldt (1874) is of the opinion that they are lobated in embryos. As the former authors mention that there are occasionally some grooves on the kidney surface, the difference between them and Toldt is perhaps chiefly in the mode of expression. The medulla is already in early stages divided into several papillae. Both of the two hog embryos that I have examined have exteriorly smooth kidneys (lengths 1.2 mm and 15 mm). The larger of these kidneys has a divided medulla. As regards the ruminants there are several investigations of the domestic animals, and Lönnberg (1903) has described some stages of antelopes. The kidneys are all smooth or slightly grooved exteriorly, and the medulla is undivided. This is also true of the sheep kidneys. *Bos*, however, which has lobated kidneys in post-embryonic life, in an early stage has both interiorly and exteriorly lobated kidneys (Toepper 1896, Hauch 1903, Petit 1924 c). In addition

to this it may be mentioned that in a cow embryo investigated by me, with kidneys only about 5 mm long, these are distinctly divided into two lobes. It is obvious that the number of the lobes increases during foetal life, as it is always relatively large later on. PETIT (1925, p. 24) mentions an embryo in *Trichechus* with quite smooth kidneys. Both in *Pinnipedia* and *Cetacea* the kidneys are lobated very early (cf. especially CHIEWITZ 1897 and OMMANEY 1932). OMMANEY describes how the number increases during foetal life in *Balaenoptera*.

In the *Primates* only little is known about this subject. *Gorilla* and *Hylobates* (DENIKER 1886, p. 247 and 251) and *Anthropopithecus* (WESTENHÖFER 1942) seem to have undivided kidneys in the embryo stages, but one specimen only was examined of each. In Man the earliest stages of the kidneys are undivided, or only slightly divided. Early in foetal life the lobes become more distinct and more numerous; thus it is obvious that a cleavage of the kidneys occurs (cf. especially HEIDENHAIN 1937).

From the above it seems quite clear that there is no case yet reported of a simple kidney having really lobated stages. Indeed, there is abundant evidence to the contrary. Those kidneys that are lobated or have several papillae in the adults are usually lobated early in foetal life, or at any rate the medulla is divided. Thus it is evident that, far from supporting the opinion that lobulated kidneys are primitive, the ontogenetic development of the mammalian kidneys indicates that the simple kidney is primitive and the lobulated kidneys have developed from undivided ones.

The phylogenetic development of the mammalian kidney types.

The reviews of the kidney form of the different orders show that the simple kidney with one papilla is the primitive type in the following groups: *Monotremata*, *Marsupialia*, *Insectivora*, *Chiroptera*, *Dermoptera* (GERHARDT 1914), *Pholidota*, *Xenarthra*, *Rodentia*, *Carnivora fissipedia*, *Hyracoidea*, *Tubulidentata* (HYRTL 1872), and *Primates*. In *Pinnipedia* and *Cetacea* there are only renculi kidneys, and it must be considered most probable that this type is primitive in these groups. The same applies to *Proboscidea*. In *Artiodactyla* either the crest kidney or the kidney with papilla is the most primitive type. Among the *Perissodactyla* and *Sirenia* there occur different types, but their distribution within the orders gives no clue to the primitive condition from which these types may be derived.

Renculi kidneys and lobated kidneys occur in *Carnivora (Ursus, Lutrinae)*, *Pinnipedia*, *Cetacea*, *Proboscidea*, *Artiodactyla (Bovinae)*, *Perissodactyla (Rhinocerotidae)*, *Sirenia (Rhytina)*, *Primates (Homo)*. It seems

very improbable that these forms should possess a kidney type more primitive than all other mammals. The occurrence in several isolated, in many respects secondarily modified types speaks strongly against the primitiveness of the renculi kidney. This is the more evident as all these forms are either large or aquatic animals.

On analogous reasons it is highly improbable that the kidney with several papillae or with tubi maximi is primitive.

If all the mammalian groups are considered there can be no doubt that the simple kidney with one papilla is the most primitive type existing, and represents the type occurring in the ancestor common to all mammals. The exclusive occurrence of simple kidneys in *Monotremata*, *Marsupialia* and several monodelphian orders is especially important in this respect, and very cogent reasons would be needed for abandoning this view, firmly based on comparative morphologic facts as it is. As shown above (p. 399) the embryology, too, supports this view.

If it is thus considered proved that the simple kidney with a papilla is the original type in the mammals, one can with more assurance trace the modifications to which the mammalian kidney has been subjected.

The crest kidney is easily derived from the kidney with a papilla, by shortening the papilla. This derivation has been assumed by as early scholars as Gegenbaur (1901) and Gerhardt (1911, 1914). There are a great number of transitional forms between these types, and this transition must be considered to have occurred independently in most mammalian groups. The crest is usually of moderate length, but is sometimes very long, as in *Giraffa* and *Halicore* (where, however, it is divided into two parts).

The kidney with tubi maximi seems usually to have developed from the crest kidney. This is probably the case with the kidneys of this type in the *Artiodactyla* and *Perissodactyla*. Tubi maximi have probably developed in a kidney with papilla in some instances, e. g. *Coelogenys*. There are numerous transitional stages towards the tubi maximi kidney (*Dasyprocta*, *Rangifer*, *Hystrix*, *Papio*). The *Hippopotamus* kidney shows an extreme development of this type, as here the tubi maximi are branched. In the elephant tubi maximi occur in the renculi. Tubi maximi have obviously developed independently in several groups: In *Simplicidentata* (probably more than once), *Dicotyles*, *Hippopotamus*, *Tragulus*, *Cervidae* (perhaps in several groups), *Perissodactyla*, *Elephas*, *Macacus*.

The type with several papillae has usually originated from the crest kidney, too, but seems also to have been derived from the kidney with one papilla. The former condition obtains in *Sus* and *Phacochoerus* and apparently in *Gorilla* and *Anoa*, the latter in *Castor*,

The *Anoa* kidney leads on towards the renculi kidney. Another stage

in this development is represented by the cow kidney. It seems most probable that all renculi kidneys have developed via the type with several papillae but undivided cortex, but it is, of course, possible that an entirely simple kidney has been divided at once into renculi. There is no evidence as to this; such a process could, however, hardly be traced now if it had taken place in the past. The renculi kidney shows a spectacular further modification in the *Cetacea*, where the number of the

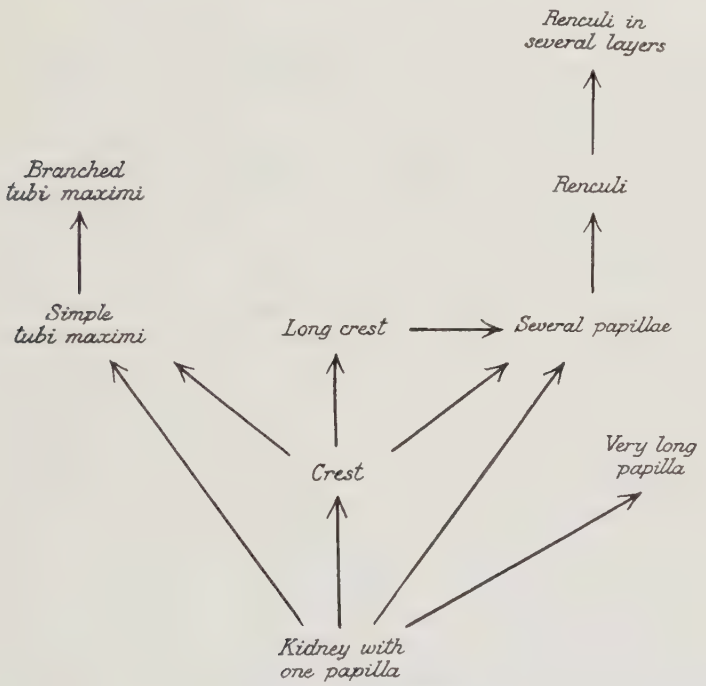


Fig. 27. Scheme of the phylogenetic development of the mammalian kidney types.

renculi is much increased and the renculi are arranged in several layers. The renculi kidney seems to have developed independently in several groups (cf. above).

The derivation of the kidney types is shown in fig. 27.

As is shown by the above the kidney has developed along a large number of parallel lines. This may be considered to be the most outstanding feature in the phylogenetic development of this organ. This makes the kidney little suited for a basis to phylogenetic conclusions, as far as the large groups are concerned. It seems, however, as if the kidney structure might well play a part in the discussion of the phylogeny of certain smaller groups.

The distribution of the kidney types in relation to size.

The distribution of the kidney types is relatively irregular in phylogenetic respects. The distribution is, however, regular as regards the size of the kidneys. In table 47, p. 415, the dimensions of the kidneys of all species examined by me have been tabulated, together with some measurements from the literature. As a more accurate measure of the kidney size the cube root of the product of the dimensions has been calculated and tabulated under the heading "Kidney size". This measure has been chosen, as the weight of the kidneys is not known either in my own alcohol kidneys or in most data from the literature. In fresh kidneys the product of the dimensions is, however, almost exactly proportional to the kidney weight (the weight of both kidneys in gms is nearly equal to this product given in ccs). Thus this product must be regarded as a good expression for the size of the kidney, and its cube root for the linear size.

From table 47 it is evident that, when the kidney size in the *Monodelphia*[1] is less than about 2 cm, the kidney almost always has a papilla. Exceptions are *Desmana*, *Aplodontia* and *Hydromys*, whose kidneys lie between the one-papilla kidney and the crest kidney. Kidneys with a size between 2 and 3 cm usually have one papilla (or a short crest), but striking exceptions are *Myocastor* and *Tragulus*. Typical kidneys with papilla do not occur among kidneys larger than 4 cm. This type thus occurs only in small animals, and is almost the only kidney type there. The exceptions occur usually in animals with more or less aquatic habits. *Tragulus* is an exception to this rule. This may, of course, be only a chance deviation, but it seems not impossible to give another explanation. The nearest relation of *Tragulus*, i. e. *Hyemoschus*, which is considered more primitive than *Tragulus*, is larger than *Tragulus* and leads a more water-loving life. It seems possible to assume that the ancestors of *Tragulus* have been larger and lived in a more moist habitat than does *Tragulus*. According to this view the kidney form of *Tragulus* could be explained as a character retained from an earlier stage of phylogenetic development.

Kidneys with a short or a moderately long crest are usually about 3—6 cm, but the large *Felidae* are forms with relatively large kidneys with a short crest.

[1] To make the material more homogenous the *Monotremata* and *Marsupialia* have been excluded from the following discussion of the kidney form, but they seem to agree in essentials with the *Monodelphia*, though the small size range in the former groups makes it difficult to ascertain this.

The large kidneys belong to the remaining types: namely, the kidneys with long crest, with several papillae, with tubi maximi, and the renculi kidneys. Among the very largest (*Cetacea*, *Rhytina*) there are only renculi kidneys with several layers of renculi. The extreme development of the kidney with tubi maximi in *Hippopotamus* and the longest crest kidneys in *Halicore* and *Giraffa* also occur in large animals.

It is evident that the kidney with one papilla occurs almost exclusively in small animals[1] and that the fairly long crest is mainly confined to animals of moderate size. The remaining types occur most often in large animals. There are exceptions, but in these cases the aberrant kidneys usually belong to aquatic animals (*Desmana*, *Hydromys*, *Myocastor*, *Coelogenys*, *Castor*, *Lutra*). Thus, there is a clear relation between kidney form, and size and habits of the animals. The fact that almost all small mammals have simple kidneys, usually with a distinct papilla, very much supports the opinion that this type is primitive. It seems to be generally agreed that the most primitive mammals were small and that, in most orders, there has been a successive increase in size. There is no reason to think that the small mammalian ancestors should not have had simple kidneys, when all mammals of similar size now living show this feature.

The relative thickness of cortex and medulla.

In table 47, p. 415, are given figures expressing the relative thickness of cortex + medulla, medulla, and cortex + outer zone. These figures have been obtained by dividing the absolute thicknesses of these layers (in mm) by the size of the kidney (in cm). If a kidney is enlarged without alteration of its structure the relative thicknesses are unaltered, but any change of the kidney structure affecting the relative thickness of its layers is indicated by these figures. The following summary of the data of table 47 as regards the Monodelphia shows roughly how the relative thicknesses are distributed among the types. The means are bracketed.

In this review the types have been subdivided according to the degree of development of their special characters. Among the crest kidneys are included the transitional forms to this type. It is apparent that the types show different relative thicknesses of the layers. There is, however, great variability within the groups. This is due to the fact that not only the kidney type but also other factors influence the thickness of

[1] The mean size of the kidney with a long papilla is 6.8 ± 0.72 mm, that of the kidney with a moderate papilla 16.1 ± 1.65 mm. The crest kidney (incl. transitional forms) is 40.4 ± 3.86 mm, the kidney with tubi maximi 50 mm (8 data), the kidney with papillae 68 mm (7 data), the renculi kidney 84 mm (7 data).

Kidney type	Cortex + medulla, rel. thickness		Cortex + out. zone, rel. thickness		Medulla, rel. thickness	
Long papilla	7.7—12.3	(10.3)	3.5—5.7	(4.2)	6.2—10.7	(8.3)
Papilla	5.7—8.9	(7.2)	2.4—5.8	(3.8)	3.5—6.8	(5.3)
Crest	4.5—6.4	(5.6)	1.7—5.7	(3.2)	2.6—4.8	(3.8)
Long crest	2.5—3.6				1.9	
Tubi	3.8—6.7	(4.97)	2.9—9.6	(4.2)	2.1—3.9	(2.9)
Branched tubi	1.8		1.8		1.0	
Papillae	3.7—5.8	(4.5)	2.2—5.8	(4.1)	1.6—3.9	(2.6)
Lobes and few renculi	2.4—4.0	(3.15)	1.8—2.4	(2.1)	1.2—3.0	(2.3)
Renculi	0.9—2.7	(1.7)	0.5—1.6	(0.9)	0.7—1.9	(1.3)

the layers. Flattened kidneys show relatively high values (e. g. *Gulo* and *Castor*). The occurrence of very thick cortices (in species with cortical nephrons) and the absence of an inner zone influence the figures. This seems to be the reason why the kidneys with tubi or papillae have high relative cortex thicknesses, as most members of these groups have cortical nephrons. In addition to these factors, the deformation of some kidneys during preservation also adds to the variability. In the groups with tubi and renculi there is undoubtedly a relation between the development of the tubi and the number of the renculi, and the relative layer thickness.

When regard is paid to these factors it is apparent that the simple kidney has high figures. The medulla is especially deep in forms with long papilla. The joint thickness of all layers, and of the inner zone, is decreased relatively in the crest kidney, and this process continues in the kidneys with tubi maximi, papillae and long crest, to reach its maximum in kidneys with numerous renculi. The cortical thickness decreases less regularly, but on the whole in a similar way.

The relation of relative layer thickness and size is shown in fig. 28. In these diagrams animals living in deserts and other arid habitats are marked with crosses, acquatic animals with circles, and the others with dots. Under the arid group have been classed *Macroscelides*, *Dipodomys*, *Pedetes*, *Jaculus*, *Gerbillus*, *Meriones*, *Psammomys*, *Dolichotis*, *Ctenodactylus*, *Camelus*, *Antilope*, *Connochaetes*, *Giraffa*, *Hyaena*, *Felis leo*. The inclusion of some of these might be questioned, and some others, for example *Hystrix cristata*, could perhaps be included, but such changes could have little influence upon the general picture.

The relative thickness of the layers diminishes clearly with increasing kidney size. The arid group has high values, especially for the medulla, and the aquatic group has, on the whole, low ones (cf. p. 389).

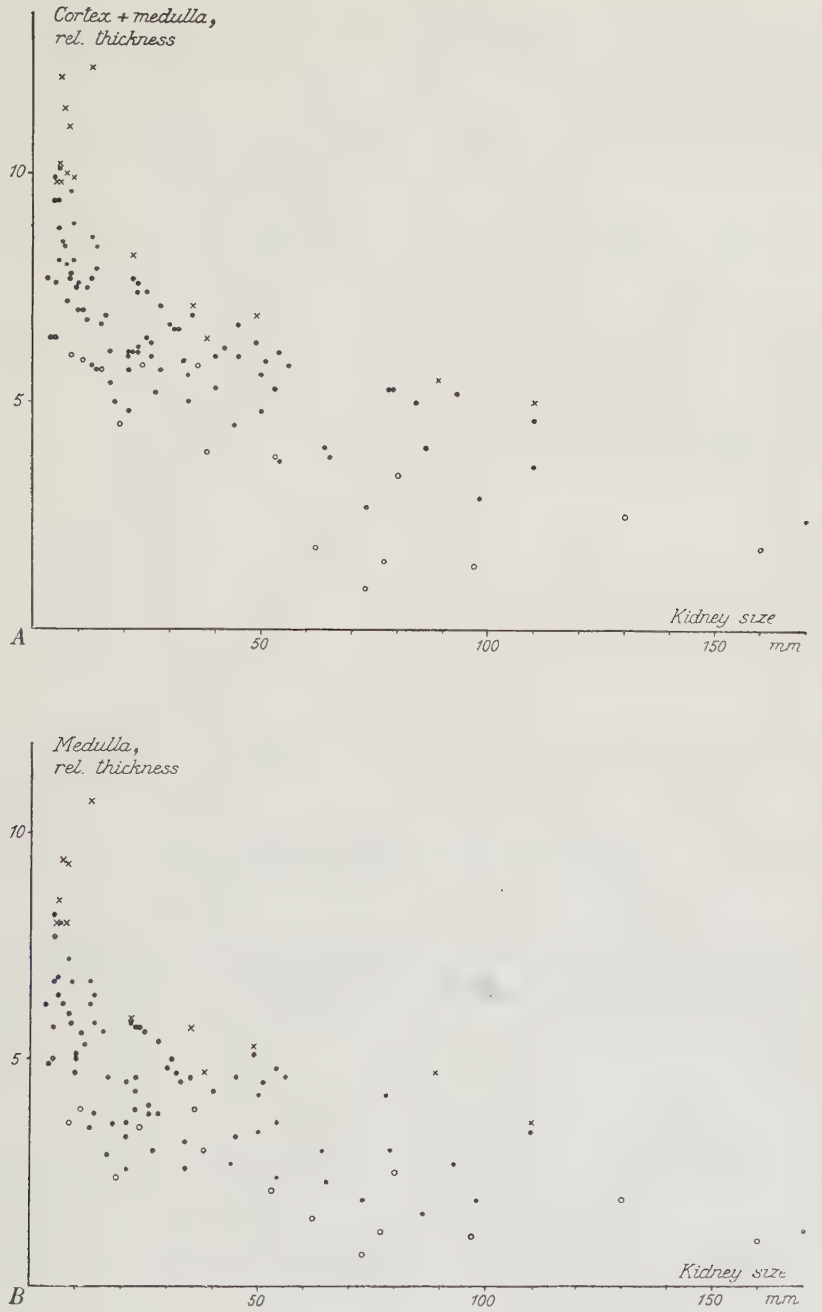


Fig. 28. Diagrams showing the relation between the relative thickness of *A* cortex + medulla, *B* medulla, and the kidney size.
Arid forms designated by crosses, water-loving forms by open circles.

As the relative layer thickness is highest in the least modified kidneys, it is easy to understand that the desert forms with their high medulla thickness have less modified kidneys than most other forms. The aquatic forms, on the other hand, which have low medulla thickness, usually have more modified kidneys than other mammals of equal size.

The relation of the length of the proximal tubule and the kidney size.

It has previously been shown that the length of the proximal tubule is closely related to the thickness of cortex and medulla (p. 377). It is then natural that this length should show a connection with the kidney size similar to that shown by the layer thickness.

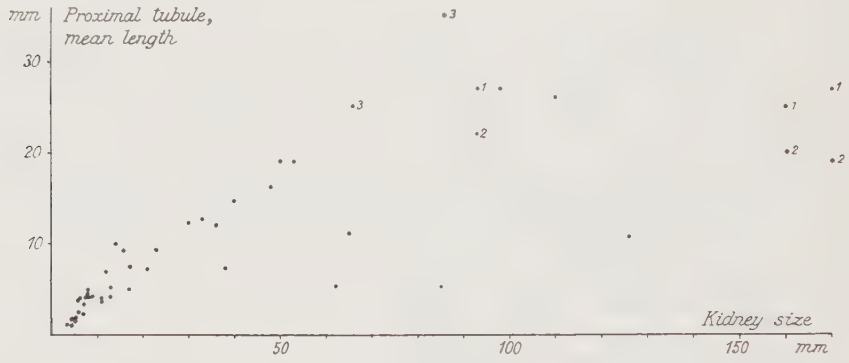


Fig. 29. Diagram showing the relation between the mean proximal tubule length and the kidney size. 1. Cortical nephrons not included. 2. Cortical nephrons included. 3. *Sus scrofa dom.*, young and old specimen.

In fig. 29 the mean length of the proximal tubule is plotted against the kidney size. The data are tabulated in table 48, p. 419. In calculating the mean length the cortical nephrons in large animals have been regarded (dots marked 2), or disregarded (dots marked 1). In small kidneys (which are simple, with a papilla or a crest) the proximal tubule increases rapidly in length with increasing kidney size. Among these kidneys there seems to be an almost linear relation between proximal tubule length and kidney size. When the kidney size has reached 40—70 mm (kidneys of this size are usually modified) this relation ceases, and in large kidneys there seems to be no or slight further increase in the length of the proximal tubules. The extreme renculi kidneys in marine carnivores have very low values.

Thus, the proximal tubule length shows similar conditions to the layer thickness. In large kidneys it is sometimes comparatively more reduced than the thickness of the cortex. This feature is especially

prominent when cortical nephrons are included in the means (dots marked 2). This is due to the fact that the high nephrons are no longer dependent on cortical thickness, as they do not reach the medulla (cf. p. 376).

The general picture is somewhat obscured by the carnivores and insectivores usually having relatively shorter nephrons than the herbivores. As the former are usually small or middle-sized forms (except the marine carnivores) the small kidneys show more varying proximal tubule length than if the herbivores are considered alone. If this is done, the relative shortness of the proximal tubules in the large kidneys is still more striking.

The marine mammals examined show very low proximal tubule lengths, which is connected with the great number of renculi in their kidneys. This may indicate that aquatic carnivores tend to have much shorter proximal tubules than terrestrial forms. *Neomys*, *Desmana* and *Lutreola* have, however, tubule lengths comparable to those of other carnivores and insectivores. *Lutra*, on the other hand, has comparatively short tubules, and *Latax* and the American *Lutra* (p. 333, foot-note) no doubt have still shorter ones, as they have numerous renculi. Thus, it would seem that all carnivores strongly adapted to water-life have shorter proximal tubules than other mammals of equal size.

Among the herbivores the aquatic forms examined do not seem to have unquestionably shorter proximal tubules than similar terrestrial forms. The *Sirenia* have not been investigated in this respect, but it is not probable that they have especially short tubules (perhaps with the exception of *Rhytina*, which had numerous renculi).

As shown on p. 375 the deepest proximal tubules are much longer than the average in small kidneys, but in the middle-sized kidneys they are not. The longest proximal tubules must, then, become shortened relative to kidney size in comparatively small kidneys, where the mean proximal tubule length is still directly proportional to kidney size.

Discussion of factors limiting the tubule length.

The facts given above show that there is a connection between the proximal tubule length and the form of the kidney. The length of the nephrons seems to be limited. It might be supposed that this limitation of the tubule length is only a consequence of the modification of the kidney form, which is determined by other factors. It seems, however, difficult to find such other factors. The surface of the kidney is certainly not essential in this respect (cf. p. 395). The frequent superficial fusion of the renculi and lobes (*Pinnipedia*, *Bos*, *Elephas*, *Homo*) con-

tradicts this explanation, as well as the assumption that large, undivided kidney masses are in themselves unsuitable in some respect. The kidneys of the elephant or the seal are very compact structures, despite their composition of renculi. The very thick cortices in forms with numerous cortical nephrons show that the thickness of the cortex is probably not essential.

On the other hand, not only the limitation of the proximal tubule mean length indicates that tubule length is of importance in itself. The longest nephrons in the small kidneys, namely the deepest ones, are relatively most shortened, and this shortening begins before any shortening of the higher nephrons is evident. In large kidneys the high proximal tubules are the longest ones. In several large herbivores these are considerably shortened by the formation of numerous cortical nephrons, which is especially noteworthy as the plan of the kidney structure is thereby upset (cf. p. 373).

If, thus, the nephron length itself is limited, it seems most probable that the limiting factor is of a physical nature. Chemical processes cannot well be directly influenced by the tubule length.

In the capsule of Bowman an ultra-filtrate of the blood is formed. The driving force of this process is the blood-pressure, opposed by the colloid-osmotic pressure of the blood and the pressure in the capsule (cf. Smith 1937 and Smith, Chasis, Goldring & Ranges 1940). The filtration is considered to result in an equilibrium between these forces, as the blood-pressure falls and the colloid-osmotic pressure rises towards the vas efferens. The pressure in the capsule is the one required to force the fluid through the tubules into the pelvis (when the pressure in the pelvis is assumed to be zero). This pressure follows Poiseuille's law. According to this law, in this case, the pressure is proportional to the volume of the fluid passing a tubule in the time unit and to the length of the tubule. The pressure is also inversely proportional to the fourth potence of the radius of the lumen.

If the lumen radius is not altered and the nephron length is increased, the volume of fluid flowing through it must be increased in the same proportion if the efficiency of the nephron is not to be diminished. Thus, the pressure in the capsule is increased proportionately to the square of the length of the nephron.

It has previously been shown that the diameter of the proximal tubule, the thick segment and the distal tubule, increases with increasing nephron length in short nephrons. This may be ascribed to the necessity of increasing the lumen width, as otherwise the pressure in the nephrons must rise rapidly. This increase in tubule diameter is, however, almost absent in longer nephrons (cf. p. 381), and in these it may be correct to

assume that the lumen width of the nephrons is constant, or at least increases very little with nephron length. Thus, in large kidneys, an increase in the nephron length must cause a rapid rise in the intracapsular pressure. If there is a considerable pressure within the capsule this must markedly diminish the filtration rate and the fraction of the plasma which is filtered. If the latter is diminished the blood flow through the glomeruli must increase, or the volume of the filtrate decreases too.

It is clear that the intracapsular pressure must be of a certain magnitude to have an appreciable effect on the filtration. If this pressure is very low the increase in it due to a moderate lengthening of the tubule can have very little importance.

The intracapsular pressure in mammals has not been measured. Brodie (1914) has given reasons for thinking that this pressure is relatively high, especially during diuresis. He has also calculated the pressure in the dog, but his calculations are no doubt erroneous (both number and diameter of the nephrons are underestimated). Smith, Chasis, Goldring and Ranges (1940, p. 756) have estimated the intracapsular pressure at about 15 mm Hg, but the basis for this estimation seems uncertain. Walker and Oliver (1941) have made direct observations of the intratubular pressure in rat and guinea-pig. They have not measured it, but state that the intratubular pressure (in the proximal tubule) was "very high", "which was particularly prominent during the infusion of hypertonic sucrose solutions" (op. cit. p. 569). On the other hand the intratubular pressure was low within the distal tubule.

It may thus be concluded that there is in the capsules of the mammals a considerable pressure that can be an important factor diminishing the filtration. If the tubule diameter is constant and the nephron length increases, the intracapsular pressure increases rapidly. If the nephrons in large kidneys were much longer than they are, the pressure in the capsules would be considerably higher. There can be little doubt that such an increase of the intracapsular pressure would reduce the efficiency of the kidneys.

It may thus be assumed that the factor limiting nephron length in large mammals is the pressure required to force the fluid through the nephrons.

The relative shortening of the nephron length in large mammals is effected either by the occurrence of cortical nephrons or by the modification of the kidney form, or by both these means.

The occurrence of the modified kidney types in freshwater forms seems, on the other hand, mainly to be due to the diminished thickness of the medulla (cf. p. 404). It is, however, probable that the volume of the fluid passing through the nephrons (at least their distal parts) is larger

in aquatic forms than in terrestrial ones. This would tend to rise the pressure in the capsule and thus to limit the nephron length.

As pointed out above, the examined *Cetacea*, *Pinnipedia* and *Lutrinae* have very short nephrons. The marine mammals apparently do not excrete particularly large volumes of water (Irving, Fisher & McIntosh 1935, Smith 1936). That their kidneys are strongly modified is natural, as they are large animals, but the fact that the nephrons are much shorter than in other mammals of equal size would seem to require a special explanation. It may, of course, be only coincidence that these aquatic carnivores are similar in this respect, but this does not seem very probable. There seem, however, to be some special features in the physiology of diving animals worthy of mention in this connection. In the seal very little urine is formed when the animal has not eaten for some time, but both volume and concentration are much increased after a meal (Smith 1936). The urine volume is thus relatively higher at some periods than it would be with a more uniform flow of urine. Further, during diving the blood flow to most of the organs of the seal is assumed to stop to a great extent (Irving, Solandt, Solandt & Fisher 1935, Irving 1939). This must also tend to increase the urine volume during the periods of renal activity. The blood-pressure changes rhythmically in the seal, also when not diving. It seems possible that the rhythm of blood-pressure is accompanied by a similar rythm in kidney function, and this further increases the filtration rate and the urine volume necessary at top activity of the kidney. This concentration of the kidney activity to certain periods may have some connection with the high relative kidney weight in the marine mammals (Denzer 1935). It is, of course, difficult to say definitely what influence this increased top activity of the kidney in the diving mammals will have upon the filtration in the capsule. It would, however, seem that the blood flow to the kidneys during certain periods should be relatively larger in the diving animals than in other mammals, where it already constitutes a large part of the total blood flow. It would then be more necessary to avoid any interference with the filtration process — especially with regard to the magnitude of the filtered plasma fraction — and thus to have short nephrons. It is of course also possible that other factors are at work, such as diminished tubule diameter, or increased volume of filtrate, but to my knowledge there are no data available which indicate such circumstances.

The evolutionary mechanism of the phylogenetic development of the mammalian kidney types.

In the above account attention has repeatedly been drawn to cases of parallel phylogenetic development. Such cases are the strong development of arcades in herbivores, the composition of the nephrons in herbivores and carnivores, the occurrence of cortical nephrons and the absence of long loops in several herbivores, and especially the macroscopic structure of the kidney. From the simple kidney several types have developed, each of them independently in several groups. The author has attempted to explain this mainly on the assumption that it is advantageous to have relatively short nephrons, as otherwise the pressure needed to force the fluid through the nephrons would be too high. An attempt will be made below to examine which evolutionary mechanism may be responsible for the development of the mammalian kidney types.

It seems clear from the distribution of the derived kidney types, if we regard the size and habits of the forms showing them, that they must be considered as adaptations. Most of them are, however, adaptations not to environment in the usual sense, but to the size of the animal. Some of the cases seem to be adaptations to environment, as in the aquatic types. The view of the derived kidney types as adaptations is of course strengthened by the explanation of their occurrence given above, but is by no means solely dependent on the correctness of this explanation.

It seems to me quite impossible to explain the development of these adaptations along Lamarckian lines of thought. It is clear that the relative shortening of the nephrons of a kidney must be connected with an increase in the number of the nephrons, which is obviously what occurs in the phylogenetic development. In the individual postnatal development, increased demands on the kidney are met with a lengthening of the nephrons. This is shown to be the case after unilateral nephrectomy (cf. e.g. Peters 1928) and is also the case in the individual development. Thus, there is no response in the individual comparable to the changes occurring in the phylogenetic development. It is also difficult to imagine how this could come about. The kidney of mature mammals cannot form new nephrons, and this is essential if the nephron length is not to increase with the size of the kidney. Thus, even if the possibility of splitting a kidney into parts in the mature state were admitted, it would not be possible to explain the phylogenetic development of the mammalian kidney by the inheritance of acquired characters. If the connection between the pressure in the capsule of the nephrons and the kidney form is accepted as true, it would seem so indirect that the as-

sumption of this need directly causing this change must involve the action of a regulating intellect, and thus falls entirely outside the limits of science.

It would perhaps seem possible to explain the development of the different kidney types on an orthogenetic basis. Each of them could arise through a series of mutations occurring in all members of a given species or group. This explanation, however, stands in opposition to the above opinion that the kidney types are adaptations. And even if this opinion is not accepted the main fact supporting it, namely the distribution of the kidney types, opposes the orthogenetic explanation. If the derived kidney types have developed by orthogenetic processes it does not seem possible to explain why they are predominant among mammals of large size, and especially why they do not occur among the numerous small forms (except in more or less aquatic types). This fact is all the more impossible to explain as the derived type is not uniform; were it so, it might perhaps be possible to think of it as a purely consequential phenomenon, following the increase in size more or less as a matter of course. This view seems untenable if due regard is paid to the fact that there are at least three fundamentally different types, each with a similar distribution.

It seems clear that the observed facts cannot well be interpreted on either a Lamarckian or an orthogenetic basis. On the other hand, they easily fall in with a selectionist interpretation. The distribution of the derived kidney types is quite natural if it is assumed that they are all advantageous in forms with heavy bulk or with aquatic habits. Which of the derived types has developed in a certain form must be attributed on the whole to chance. At any rate in their first stages, they seem to be similar in respect of the advantage they can offer, and as far as suitable mutations occur, are thus equivalent with regard to selection. Of course it is possible that some structural features in the ancestral type may dispose it to develop into a certain one of the secondary types, but there is no indication of this. In some orders all forms show the same kidney type, as in *Pinnipedia* and *Cetacea*; in others there are more than one of the secondary kidney types, as in *Sirenia*, *Artiodactyla*, *Perissodactyla*, *Primates*.

Finally, it is obvious that the almost complete absence of the secondary kidney types in small mammals is in conformity with the selectionist view. In this respect two views are possible. Either the simple kidney type with a papilla is the most advantageous one in small mammals, and would thus be maintained even against some mutation pressure, or it is only the absence of a sufficient advantage in the other types that has preserved the original type in small animals.

Summary.

The macroscopical structure of the kidney has been examined in about 140 species from most mammalian orders. In more than 50 species the microscopical structure has been examined after maceration, and measurements have been made on one or more parts of the nephron.

There are some facts which indicate that a terminal segment, distinct from the rest of the proximal tubule, exists not only in carnivores but probably in all mammals.

The collecting tubules with arcades are shown to be secondarily developed from collecting tubules without such. An explanation of the phylogenetic mode of development is set forth. The arcades are most often developed in herbivores, and have probably developed independently in several groups.

There are several mammals whose kidneys show no long loops (*Hystrix*, *Castor*, *Elephas*, *Hippopotamus*, *Papio*). This is almost certainly a secondary feature, developed independently in several groups of herbivores. This is also the case with the occurrence of numerous cortical nephrons.

The variation of the length of the proximal tubule within the kidney has been studied, as also the relation between the thickness of the cortex and the medulla, and the length of the proximal tubule.

The diameter of the proximal tubule increases relatively rapidly with increasing tubule length, when the latter is small or moderate (up to about 15 mm). When the length of the proximal tubule increases further, the increase in the diameter is slight. Similar circumstances are found with regard to the thick segment and the distal tubule.

The composition of the nephrons is studied in several species. It is shown that there are quantitative differences between carnivores and herbivores. Among the latter a group of 4 desert rodents deviates markedly from the others; the thin and the thick segment are lengthened.

In this connection the problem of the localisation of the water reabsorption in the nephron is discussed. The theory that the hypertonicity of the urine develops in the thin segment is not adequately founded. The comparative study of the nephron composition indicates that, though

a water reabsorption probably occurs in the thin segment, this is also the case in the thick segment, and perhaps in the distal tubule and possibly in the collecting tubules also.

The surface and volume of the segments of the average nephron have been calculated in a few species. v. MÖLLENDORFF's index is discussed.

The simple kidney with a papilla is the primitive kidney type in the mammals. From it the kidneys with crest, with tubi maximi, with papillae and with renculi have developed, each of them independently in several groups. This is not only evident from comparative anatomical facts, but is also entirely in agreement with the embryonic development of the kidneys. The cortex and the zones of the medulla are relatively thinner in kidneys of the secondary types than in the primitive simple kidney. The secondary types usually occur in aquatic or large mammals.

The proximal tubule is relatively shorter in large kidneys than in small. This indicates that the nephrons cannot increase in length as much as the increase in kidney size demands. This is probably the reason why the secondary kidney types have developed in large mammals. In freshwater forms the medullary thickness is decreased (in connection with a shortening of the relative length of the distal parts of the nephron), which seems to be the main cause for the occurrence of modified kidney types in freshwater forms.

An attempt is made to explain the limitation of the length of the proximal tubule as due to the increasing pressure in the capsule required to force the fluid through the nephron when the nephron length increases. If this pressure rises markedly it will interfere with the filtration process in the glomerulus. It seems possible to extend this explanation to the extraordinary shortness of the nephrons in some diving carnivores, and thus to explain the extreme development of the renculi kidney in the marine mammals and *Lutrinae*.

Some evolutionary aspects of the phylogenetic development of the mammalian kidney are discussed. It is concluded that the development may be explained on a selectionist basis, but hardly on an orthogenetic or a Lamarckian one.

Table 47. *Kidney type*, *kidney size* (= the cube root of the product of the dimensions), *layer thickness*, *relative layer thickness* $\left(= \frac{\text{layer thickness}}{\text{kidney size}}\right)$ *of mammalian kidneys.*

Z. = Zarnik 1910, G. = Gerhardt 1914, pap. = papilla, l. pap. = long papilla, s. pap. = several papillae, sh. cr. = short crest, cr.-p. = intermediate between crest and papilla, cr.+t. = crest+tubi maximi; the page numbers refer to descriptions in the special section; the rel. thickness is multiplied by 10.

[1] Forms with arid habitat. [2] Forms with moist habitat.

	Kidney type	Kidney size mm	Thickness in mm of			Relative thickness of		
			cortex	outer zone	inner zone	cortex + medulla	cortex + out. zone	medulla
Echidna aculeata (Z.) . . .	pap.	(21)	6	7	0	6.2	6.2	3.3
Ornithorhynchus anat.[2] . .	sh. cr.	19	4	4.5	0	4.5	4.5	2.4
Philander sp.	l. pap.	6.5						
Sminthopsis murina	pap.	5.9	1.0	1.4	2.4	8.1	4.1	6.4
Antechinomys laniger[1] . . .	l. pap.	5.5	1.0	1.5	2.9	9.8	4.5	8.0
Perameles sp.	pap.	8.3						
Sarcophilus satanicus . . .	pap.	31	5	4.5	11	6.6	3.1	5.0
Dasyurus viverrinus . . .	pap.	15		10		6.7		
Didelphys opossum	pap.	23	4	5	8	7.4	3.9	5.7
Acrobates pygmaeus	l. pap.	5.1	1.4	1.2	2.2	9.4	5.1	6.7
Petaurus breviceps	pap.	8.2						
Phascolarctus cinereus . . .	pap.	26	6	10.5		6.3		4.0
Phalangista vulpina	pap.	25	4.5	14		7.4		5.6
Macropus giganteus[1] . . .	pap.	49	8	9	17	6.9	3.5	5.3
Phascolomys mitchelli . . .	crest	35	8	16		6.9		4.6
Tupaia javanica	pap.	8.3	1.5	5		7.8		6.0
Macroscelides sp.[1]	l. pap.	7.0	1.4	2.6	4	11.4	5.7	9.4
Centetes ecaudatus (G.) . .	pap.	18						
Erinaceus europaeus	pap.	17	2.4	2.3	5.6	6.1	2.8	4.6
Sorex araneus	pap.	5.0	0.9	1.0	1.8	7.6	3.9	5.7
Sorex minutus	pap.	3.9	0.6	0.8	1.1	6.4	3.6	4.9
Neomys fodiens	pap.	5.0	0.7	0.9	1.6	6.4	3.2	5.0
Pachyura etrusca	l. pap.	3.3	0.5	0.75	1.3	7.7	3.8	6.2
Talpa europaea	pap.	8.0						
Desmana moschata[2]	p. 281	11	2.2	2.3	2.0	5.9	4.1	3.9
Galeopithecus (G.)	pap.	(21)						
Pteropus edulis	pap.	14	2.7	5.3	0	5.7	5.7	3.8
Pteropus medius	pap.	13	3	4.5	0	5.8	5.8	3.5

Table 47 (Cont.).

	Kidney type	Kidney size mm	Thickness in mm of			Relative thickness of		
			cortex	outer zone	inner zone	cortex + medulla	cortex + out. zone	medulla
Pipistrellus nilssoni	l. pap.	5.0	0.85	1.3	2.8	9.9	4.3	8.2
Vespertilio murinus	l. pap.	4.8	0.8	1.3	2.4	9.4	4.4	7.7
Oryctolagus cuniculus	pap.	28	5	5	10	7.1	3.6	5.4
Ochotona alpina	pap.	8.2		6.3		7.7		
Aplodontia rufa	sh. cr.	17	4.2	5		5.4	5.4	2.9
Sciurus vulgaris	pap.	12	1.8	2.6	3.8	6.8	3.7	5.3
Castor fiber[2]	2 pap.	36	7	14	0	5.8	5.8	3.9
Perodipus agilis[1]	l. pap.	7.5	1.5	1.7	4.3	10	4.3	8
Dipodomys m. exilis[1]	l. pap.	5.9	1.0	1.2	3.8	10.2	3.7	8.5
Heteromys adspersus	pap.	6.5		5.5		8.5		
Geomys tuza	pap.	10	2.6	5		7.6		5.0
Pedetes caffer[1]	pap.	22	5	4	9	8.2	4.1	5.9
Jaculus jaculus[1]	l. pap.	8.0	1.4	2.1	5.3	11	4.4	9.3
Spalax typhlus	pap.	7.6		5.5		7.2		
Cricetus cricetus	pap.	12		9		7.5		
Microtus agrestis	pap.	9.0	2.1	2.8	2.4	8.1	5.4	5.8
Evotomys glareolus	pap.	7.0						
Arvicola terrestris	pap.	9.5						
Neofiber alleni[2]	pap.	8.4	2	3		6.0		3.6
Epimys rattus	pap.	14	2.9	2.6	5.4	7.9	3.9	5.8
Mus musculus	l. pap.	6.1	1.3	1.2	3.7	10.2	4.1	8.0
Mus flavicollis	pap.	6.9	1.5	1.3	3.0	8.4	4.1	6.2
Mus sylvaticus	pap.	5.9	1.2	1.3	2.7	8.8	4.2	6.8
Deomys ferrugineus	pap.	7.5		6		8.0		
Gerbillus pyramidum[1]	l. pap.	6.2		7.5		12.1		
Meriones melanurus[1]	l. pap.	9.1		9		9.9		
Psammomys obesus[1]	l. pap.	13	2.1	2.4	11.5	12.3	3.5	10.7
Hydromys chrysogaster[2]	sh. cr.	15	2.7	2.1	3.7	5.7	3.2	3.9
Hystrix cristata[(1)]	crest	44	8	12	0	4.5	4.5	2.7
Atherura africana (G.)	crest	28						
Erethizon dorsatus (G.)	p. 316	33						
Coelogenys paca[2] (G.)	tubi	31						
Dasyprocta aguti	p. 316	23	5	9		6.1		3.9
Hydrochoerus capyb.[2] (G.)	tubi	53	9	11		3.8		2.1
Dolichotis patagonica[1]	pap.	35	5	7	13	7.1	3.4	5.7

Table 47 (Cont.).

	Kidney type	Kidney size mm	Thickness in mm of			Relative thickness of		
			cortex	outer zone	inner zone	cortex + medulla	cortex + out. zone	medulla
Chinchilla lanigera	pap.	13	2.5	1.7	7	8.6	3.2	6.7
Myocastor coypus[2]	sh. cr.	24	5.5	8.5		5.8		3.5
Ctenodactylus gundi[1]	l. pap.	6.1		6		9.8		
Manis javanica	pap.	23	4.5	13		7.6		5.7
Bradypus sp.	sh. cr.	23	4	10		6.1		4.3
Cyclopes didactylus	l. pap.	8.3	2	6		9.6		7.2
Dasypus sexcinctus	pap.	32	6	5	10	6.6	3.4	4.7
Felis catus	pap.	30	5.5	4	10.5	6.7	3.2	4.8
Felis leo[1] (HECKING)	sh. cr.	89	7	8	34	5.5	1.7	4.7
Felis tigris (HECKING)	sh. cr.	78	8	6	27	5.3	1.8	4.2
Felis pardus (HECKING)	pap.	49	6	6	19	6.3	2.4	5.1
Felis pardalis	pap.	53						
Felis onca	sh. cr.	56	6.5	5	21	5.8	2.1	4.6
Lynx lynx	sh. cr.	45	6.5	6	14.5	6.0	2.8	4.6
Arctitis binturong	cr.-p.	21	5	7	0	5.7	5.7	3.3
Viverra sp.	cr.-p.	21	3	2.5	7	6.0	2.6	4.5
Cryptoprocta ferox	pap.	22	4	5	8	7.7	4.1	5.9
Prionodon linsang	pap.	14	2.7	2.5	6.5	8.4	3.7	6.4
Hyaena sp.[1]	crest	54	7	7	19	6.1	2.6	4.8
Canis lupus	crest	51	7	7	16	5.9	2.7	4.5
Canis familiaris	crest	40	7	6	11	6.0	3.3	4.3
Nasua narica	pap.	26	5.5	3.5	6.5	6.0	3.5	3.8
Potos flavus	pap.	17						
Procyon lotor	sh. cr.	28	5.5	3.5	7.0	5.7	3.2	3.8
Ailurus fulgens (G.)	cr.-p.	29						
Ailuropoda melanoleuca (RAVEN)	6 lob.	57						
Ursus arctos	renc.	73	6	6	8	2.7	1.6	1.9
Mustela erminea	pap.	11	1.5	1.7	4.5	7.0	2.9	5.6
Lutreola vison	pap.	23	3.5	3.5	7	6.1	3.0	4.6
Martes martes	cr.-p.	18	2.5	2.5	4	5.0	2.8	3.6
Gulo gulo	crest	42		26		6.2		
Meles meles	cr.-p.	33	4.5	4	11	5.9	2.6	4.5
Lutra lutra[2]	renc.	38	3.5	4	7.5	3.9	2.0	3.0

Table 47 (Cont.).

	Kidney type	Kidney size mm	Thickness in mm of			Relative thickness of		
			cortex	outer zone	inner zone	cortex + medulla	cortex + out. zone	medulla
Phoca hispida[2]	renc.	62	2.2	3	6	1.8	0.8	1.5
Phoca barbata[2]	renc.	97	2.5	4	7	1.4	0.7	1.1
Otaria jubata[2]	renc.	77	2.5	3	6	1.5	0.7	1.2
Phocaena phocaena[2]	renc.	73	1.5	2	3	0.9	0.5	0.7
Balaenoptera musculus[2]	renc.		6	9	9			
Procavia capensis	pap.	16	2	4	5	6.9	3.8	5.6
Elephas maximus	renc.	170	20	20	0	2.4	2.4	1.2
Trichechus manatus[2]	p. 346	80	7	20		3.4		2.5
Halicore dugong[2] (RIHA)	p. 347	130	8	25		2.5		1.9
Rhytina stelleri[2] (STELLER)	renc.							
Hippopotamus amphibius[2]	tubi	160	12	16	0	1.8	1.8	1.0
Sus scrofa domestica	s. pap.	86	20	7.5	6.5	4.0	3.2	1.6
Phacochoerus sp.	p. 359							
Dicotyles sp.	tubi							
Camelus bactrianus[1]	crest	110	15	15	25	5.0	2.7	3.6
Lama lama, young	crest	40		21		5.3		
Tragulus javanicus	tubi	21	4.5	5.5		4.8		2.6
Cervus elaphus	cr.+t.	65	10	15		3.8		2.3
Dama dama	crest	53	9	11	8	5.3	3.8	3.6
Alces alces	crest	93	23	13	12	5.2	3.9	2.7
Rangifer tarandus	tubi	45	15	12	3	6.7	6.0	3.3
Antilope cervicapra[1]	pap.	38	6.5	5.5	12.5	6.4	3.2	4.7
Connochaetes gnu[1]	crest	50	7	21		5.6		4.2
Cephalophus melanorh.	sh. cr.	25		16		6.4		
Ovis aries	crest	50	7	7	10	4.8	2.8	3.4
Ovibos moschatus	crest	79	18	24		5.3		3.0
Anoa depressicornis	s. pap.	54	7	5	8	3.7	2.2	2.4
Bos taurus	lobes	98	9	9	10	2.9	1.8	1.9
Bison bonasus, young	lobes							
Giraffa[1] (GERHARDT 1899)	l. cr.	110		40		3.6		
Tapirus indicus	tubi	84		42		5.0		
Rhinoceros bicornis	p. 365							
Equus caballus	tubi	110	14	16	21	4.6	2.9	3.4

Table 47 (Cont.).

	Kidney type	Kidney size mm	Thickness in mm of			Relative thickness of		
			cortex	outer zone	inner zone	cortex + medulla	cortex + out. zone	medulla
Orycteropus (HYRTL 1872) .	pap.							
Lemur catta	pap.	21	5	5.5	2.0	6.0	5.0	3.6
Chiromys madagascar. . . .	pap.	13	2.5	3	5	7.7	4.2	6.2
Galago sp.	cr.-p.	27	6	8		5.2		3.0
Galago sp.	pap.	9.7	2.7	4.6		7.5		4.7
Tarsius spectrum	pap.	9	2	1.5	4.5	8.9	3.9	6.7
Hapale jacchus	pap.	10	2	5		7		5
Macacus sylvanus	tubi	34	8	11	0	5.6	5.6	3.2
Papio sp.	crest	34	8	9	0	5.0	5.0	2.6
Homo sapiens	lobes	64	6.5	19		4.0		3.0

Table 48. *Percentage of long loops, cortical nephrons, kidney size, nephron composition, index and volume index of mammalian kidneys.*

1. Corrected to correspond to the swollen tubules. 2. Corrected for shrinkage. 3. (in the cat). Composition of high nephron from table 26 k. + cortical nephrons. y. = young.

	Long loops %	Kidney size, mm	Proximal tubule, mean length, mm	High nephrons, average composition %				"Mean nephron" composition %				Prox. tubule / Thick segment	Ind.	Vol. ind.
				p.t.	t.s.	th.s.	d.t.	p.t.	t.s.	th.s.	d.t.			
Sminth. m.	24	5.9	2.0	34	14	35	16	33	28	26	13	1.24	10.8	6.8
Antechin. l.	30	5.5	2.5	35	17	36	12					1.13	10.8	4.7
Macroscel.	34	7.9[1]	4.2	42	11	38	10					1.27	10.2	5.0
Erinaceus e. . . .	39	17	5.0	41	12	33	14					1.38	14.6	7.9
Sorex a. old . . .	12	7.0	2.2	41	12	35	13	40	16	32	12	1.29	17.7	13.3
» » y.	24	5.0	1.6	39	10	36	15						11.5	7.9
» *m.*	16	4.2	1.0	40	14	34	13						11.7	9.1
Neomys f.	21	5.0	1.5	39	11	33	15	38	20	29	14	1.31	9.7	5.7
Pachyura e. . . .	18	3.3	1.1	36	14	35	15	34	23	30	12	1.12	12.9	10.7
Desmana m. . . .	5	11	4.0[2]										13.4	6.0
Pteropus e.	0+	14	3.8	58	2	21	19						15.1	9.5
Pipistr. n.	25	5.0	1.8	33	15	36	17					1.20	6.5	2.9
Vespert. m. y. . .	27	4.8	1.8	36	13	35	17					1.08	6.9	4.0
» » ad. . .	36	5.5	1.8					30	25	31	14	0.96	9.0	5.8

Table 48 (Cont.).

	Long loops %	Kidney size, mm	Proximal tubule, mean length, mm	High nephrons, average composition %				"Mean nephron" composition %				Prox. tubule / Thick segment	Ind.	Vol. ind.
				p.t.	t.s.	th.s.	d.t.	p.t.	t.s.	th.s.	d.t.			
Oryctol. c. ♂ 10 m. .	48	27	16.2	55	9	29	7	56	13	25	6	2.25	30.0	14.5
» ♀ 10 m. . .	46	28	16.7	58	7	27	8	54	16	24	6	2.23	23.0	9.1
Sciurus v.	57	12	6.9	54	9	29	9					2.00	18.9	10.9
Castor f.	0+	36	12[2]										25.6	13.8
Perodipus a. . . .		9.0[1]	4.1	40	16	34	10					1.40	16.4	8.9
Dipodomys m. . .	27	5.9	2.4[2]	40	18	34	8	38	25	29	7	1.29	14.7	6.9
Jaculus j.	33	8	4.5	37	18	38	7					1.18	18.6	9.5
Microtus a. ♀ . . .	14+	7.7	4.1	57	2	30	12	56	8	25	10	2.28	7.9	3.0
» » ♂ . . .	8+		4.5	55	3	33	9					1.57	20.0	14.5
Evotomys g.	+	7.0	3.3	61	1	24	13						19.2	12.9
Epimys r.	28	14	10	54	10	30	8					1.87	18.9	8.4
Mus musc.	24	6.1	4.0	56	7	29	8					2.15	16.9	9.9
Mus flavic. ♂ . . .	27	7.5	4.0	52	6	32	10	53	11	28	9	1.90	13.9	7.3
» » old ♂ . .	23	8.1	4.7	53	6	31	10	51	11	29	9	1.74	19.2	11.7
Mus sylv.	17	5.9	3.9	51	8	28	13					2.12	15.3	7.8
Hydromys chr. . .		17	7.5									1.83	28.5	16.4
Psammomys o. . . .	100	13	4.2									0.91	10.5	5.1
Hystrix c.	0+	33[1]	12.6									1.43	17.9	7.7
Felis c. y. ♀ 66 gm[3].	100	24	5.8	44	27	29	7	34	30	27	9	1.30	16.5	8.2
» » ♂ 17 gm.	100	32	18					47	21	24	8	2.00	52.6	37
Arctitis. b.	0+	21	7.1[2]	54	1	30	16					1.63	14.1	5.9
Canis f.	100	40	14.8	44	20	27	9	41	27	23	9	1.78	22.2	9.4
Ursus a.	17	65	11	50	8	28	15	50	13	25	11	2.00	20.1	8.7
Mustela e.	95	11	3.8	42	15	31	12					1.58	15.2	9.1
Lutreola v.	74	23	9.2	40	13	34	13						12.2	4.8
Lutra l. ♀		38	7.4	45	15	32	9						12.0	4.7
» » ♂	46	32	6.8	45	12	32	12						14.8	7.0
Phoca h.	42	62	5.2	42	14	35	9	39	26	28	7	1.38	10.5	4.2
Phoca b.	68	126[1]	10.7	35	21	33	7					1.18	13.5	5.3
Phocaena ph. . . .	34	85[1]	5.1	40	16	35	9					1.28	9.5	4.0
Balaenopt. m. . . .	37		13.3	39	20	35	6					1.15	16.2	6.1
Procavia c.	17	16	9.2[2]										14.1	5.1
Elephas m.	0+	170	19	55	2	23	21						8.2	2.2

Table 48 (Cont.).

	Long loops %	Kidney size, mm	Proximal tubule, mean length, mm	High nephrons, average composition %				"Mean nephron" composition %				Prox. tubule / Thick segment	Ind.	Vol. ind.
				p.t.	t.s.	th.s.	d.t.	p.t.	t.s.	th.s.	d.t.			
Hippopot. a.	0+	160	20	60	0	27	13						12.5	3.6
Sus s. old ♀	3+	86	35	73	0	16	11	68	4	17	12	4.0	20.2	5.3
» » y.	+	66	25										22.4	8.7
Camelus b.	55	110	29	49	11	35	6					1.26	18.7	5.1
Dama d.		53	19										14.7	4.3
Alces a.	+	93	22										17.8	7.4
Rangifer t.	+	45	21[2]										21.9	7.7
Ovis a.	36	50	19	52	10	32	6						18.9	5.6
Bos t.	21	98	27	56	8	25	11	50	13	28	9	1.80	17.7	5.2
Equus. c.	19	110	26[2]	53	10	32	5	51	14	29	6	1.73	19.8	6.3
Chiromys m. . . .	24	13	5.1	43	12	35	12					1.50	12.8	5.9

Table 49.

	Average nephron		Average nephron (excl. capsule)								Total kidney weight gm	Total nephron number	Author	$\frac{n \times v}{1000}$
	Surface sq. mm	Volume cmm v	Surface of the segments %				Volume of the segments %							
			p.t.	t.s.	th.s.	d.t.	p.t.	t.s.	th.s.	d.t.		n		
Sorex araneus	0.5015	0.004233	57	4.7	25	13	69	1.1	18	13	0.35	82000	Denzer 1938	0.35
Neomys fodiens . . .	0.2726	0.001729	53	5.8	25	16	64	1.5	19	16	0.19			
Rabbit, male 10 m . .	4.327	0.06258	77	2.7	15	4.8	88	0.5	7.9	3.3	22	315000	Nelson 1922	19.7
» *, female 10 m* .	4.133	0.05179	72	5.5	16	6.1	84	1.6	9.7	5.0	24	315000		16.3
Dipodomys m. exilis			51	12	29	7.8	61	5.5	26	7.4				
Mus flavicoll. male .	0.7764	0.007096	68	3.1	21	8.6	78	0.8	14	7.2	0.42	72000	Denzer 1938	0.51
Dog	4.449	0.05305	60	11	20	8.6	74	3.6	15	7.0	77	800000	Kunkel 1930	42.4
Cow	7.823	0.1112	69	5.3	19	7.3	82	1.9	11	5.0	1000	8000000	» »	890

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Explanation of the plates.

Plate 1.

Fig. 1. *Sminthopsis murina*, high nephron. 25 ×.
Fig. 2. *Sminthopsis murina*, deepest proximal tubule. 25 ×.
Fig. 3. *Sminthopsis murina*, deep nephron. 25 ×.
Fig. 4. Rabbit, old female, high proximal tubule. 25 ×.
Fig. 5. *Epimys rattus*, middle high proximal tubule. 25 ×.

Plate 2.

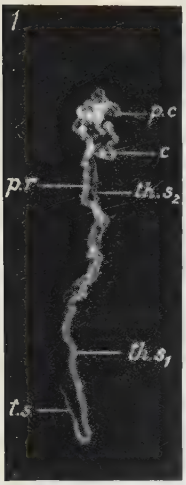
Fig. 1. *Hystrix cristata*, young, deepest nephron. 25 ×.
Fig. 2. *Mus flavicollis*, high nephron. 25 ×.
Fig. 3. The same nephron as in fig. 2, showing the segments in their original position. 25 ×.
Fig. 4. *Phoca hispida*, kidney. 1 ×.

Plate 3.

Fig. 1. *Sorex minutus*, high nephron. 75 ×.
Fig. 2. Rabbit, distal tubule with adjoining parts. 50 ×.
Fig. 3. Dog, distal tubule with adjoining parts. 50 ×.

List of the abbreviations of the plates.

a	transition into the terminal part of the proximal tubule.
c	Bowman's capsule.
c. d	collecting tubule.
d. t	distal tubule.
i. s	intercalated segment.
i. t	initial collecting tubule.
p. c	pars convoluta of the proximal tubule.
p. r	pars recta of the proximal tubule.
t. s	thin segment.
th. s	thick segment.
th. s_1	thicker part of the thick segment.
th. s_2	thinner part of the thick segment.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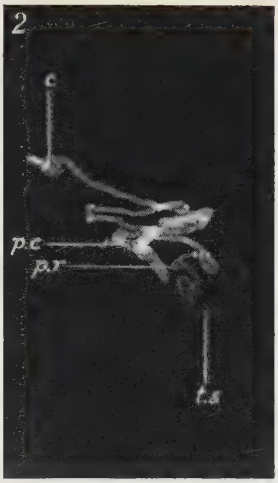
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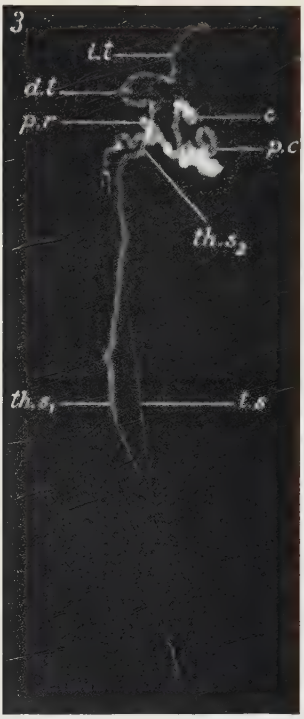
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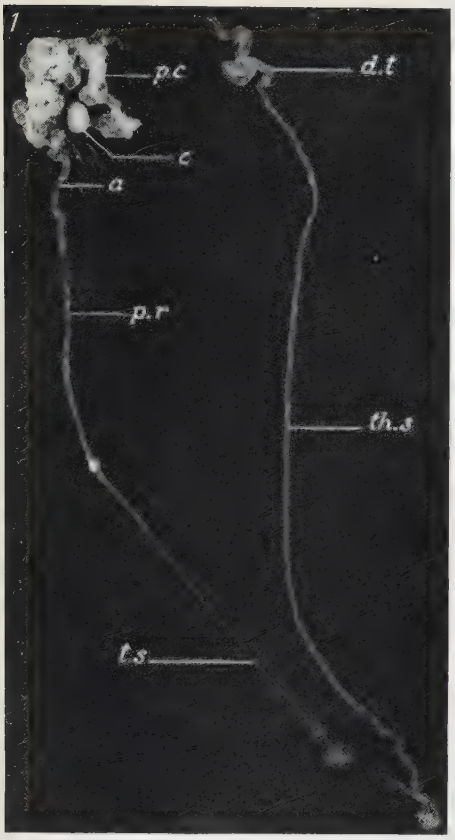
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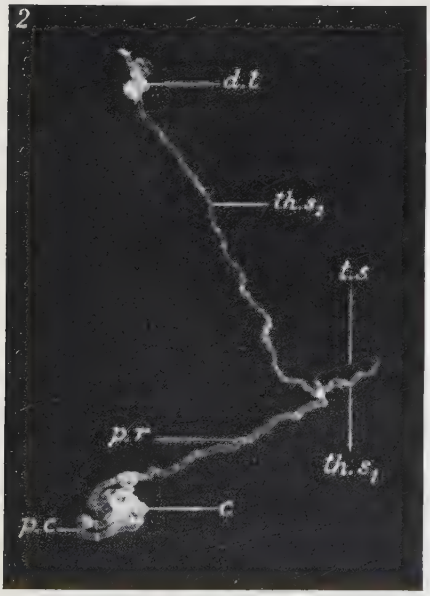
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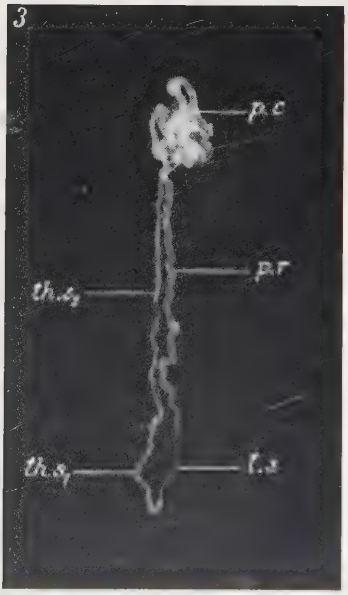
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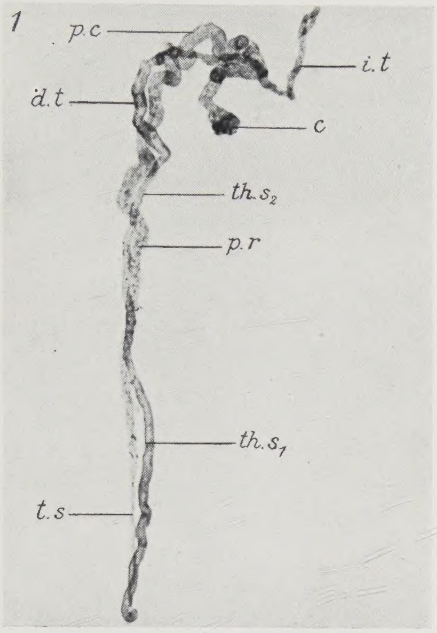
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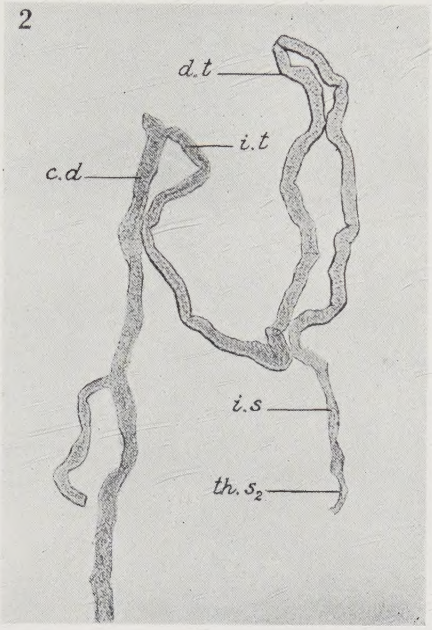
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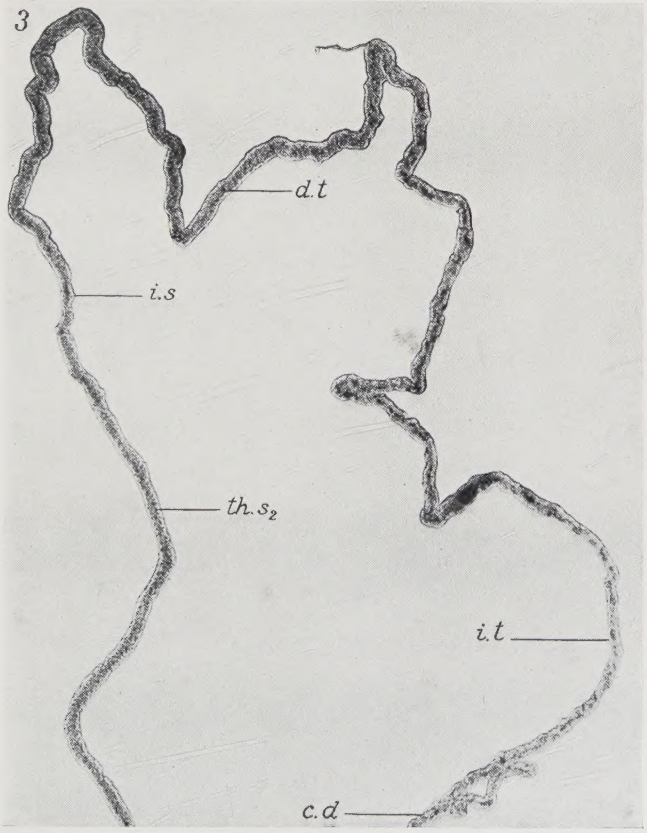
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